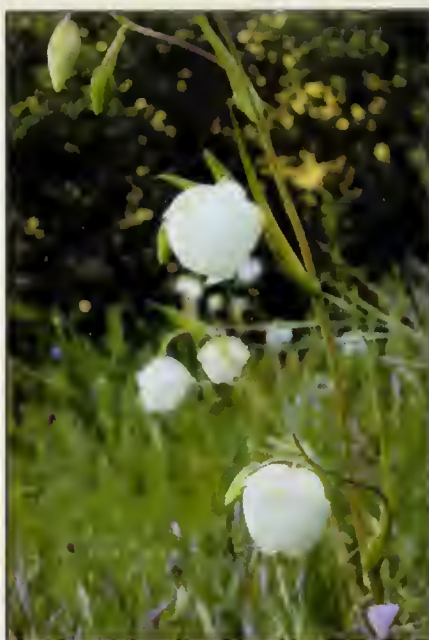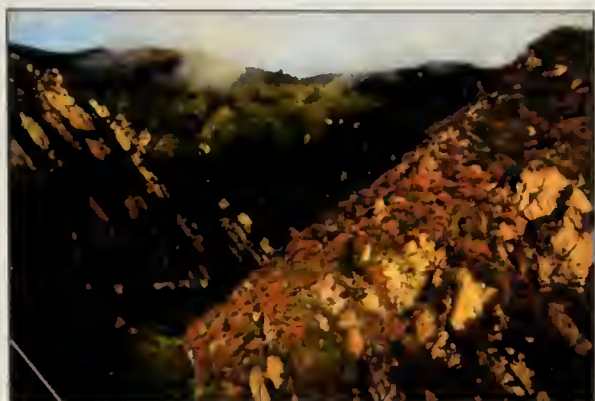Proceedings of the 32nd Annual Southern California Botanists Symposium

Flora and Ecology of the Santa Monica Mountains

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Edited by:
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Preface

The Santa Monica Mountains, with their rich flora and fauna, are a globally significant example of the diverse Mediterranean-climate ecosystem, designated as one of the world's biodiversity "hotspots." The threats to this biodiversity are great, including impending development, fragmentation, invasive species, increasing fire frequency, nitrogen deposition, altered hydrology, climate change, and the interacting and cascading effects of all of these factors. The 150,000-acre Santa Monica Mountains National Recreation Area, the nation's largest urban park, provides crucial open space in one of the United States' largest urban areas. In this network of city, county, state, federal, and private landholders, the conservation challenges are immense, while the opportunities for education and volunteerism provide hope.

These proceedings are the product of the Southern California Botanists' one-day annual symposium held at California State University, Fullerton, on October 28, 2006. It provides a valuable cross-section of both baseline floristic and ecological information, and it is our hope that it will be an important reference for the region.

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SANTA MONICA MOUNTAINS: BIOGEOGRAPHY AND CULTURAL HISTORY

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ABSTRACT: The Santa Monica Mountains of southern California are a small but rugged anticlinal mountain range bordered on the south by the Pacific Ocean and extending 70 km from the Oxnard plain (Ventura County) in the west to the City of Los Angeles in the east. They are 5 to 21 km wide and crest at an average 450 to 600 m (948 m maximum) elevation. They experience a typical wet winter – dry summer Mediterranean-type climate with high year-to-year precipitation variability. Despite their location within the second largest population center in the nation, the Santa Monicas retain 80% native vegetation cover and are vegetationally very diverse, containing some of the best remaining chaparral and coastal sage scrub in coastal southern California. The gentle climate and biologic richness of the Santa Monica Mountains made them attractive to native Chumash and Gabrielino/Tongva peoples and their occupation is marked by over 1,000 archeological sites. Europeans also found the surrounding valleys and Los Angeles Basin attractive for settlement, and the explosive growth of the Los Angeles area in the last century threatens the ecological integrity of the Santa Monicas. In response to this threat the Santa Monica Mountains National Recreation Area (61,000) was created in 1978 and today approximately half the lands (30,000 ha) within it are protected by public and private parks and conservation agencies. Still, many threats to the integrity of the ecosystem remain. Some threats come from loss of habitat and connectivity due to development of private lands within the mountains. Others, such as the occurrence of overly frequent fires leading to vegetation type conversion, are exogenous, arising in the surrounding urbanized environment.

KEYWORDS: Chumash, climate, Gabrielino, geography, geology, land management history, native peoples, Santa Monica Mountains, conservation threats, Tongva, vegetation, wildlife

INTRODUCTION

The Santa Monica Mountains are a unique natural island within urbanized coastal southern California. They bisect the City of Los Angeles, separating downtown from the San Fernando Valley, and include the entire city of Malibu. It is estimated that 17 million people live within one hour's drive of the range. Despite the extensive urban development surrounding and within the Santa Monica Mountains, they retain much of their natural character, with greater than 80% of the land cover containing native vegetation. The mountains contain some of our best remaining stands of coastal sage scrub and chaparral, as well as live oak woodlands, valley oak savanna, and coastal salt marsh (Figure 1). The high habitat diversity, coastal situation, and moderate Mediterranean climate were attractive to aboriginal peoples; their occupation is evidenced by over 1,000 identified archeological sites. These same characteristics were attractive to European
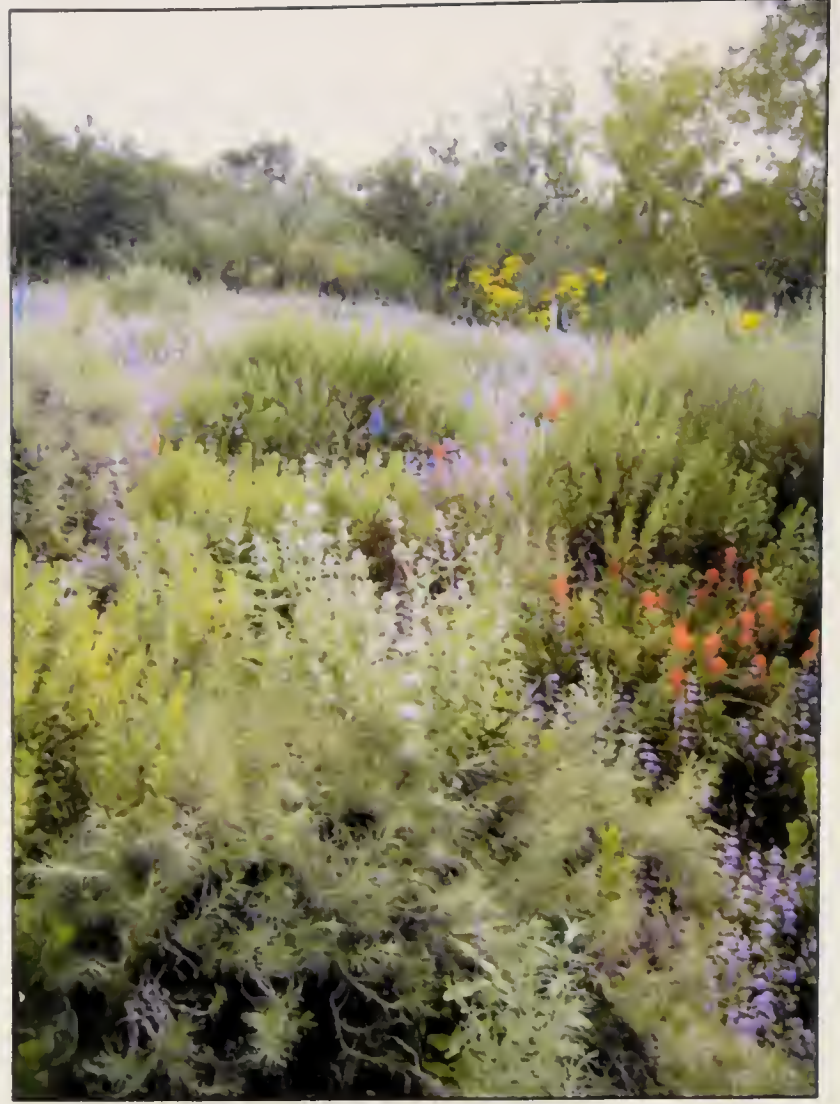
Figure: 1a. Chaparral in Mugu State Park.   **1b.** Typical coastal sage scrub.
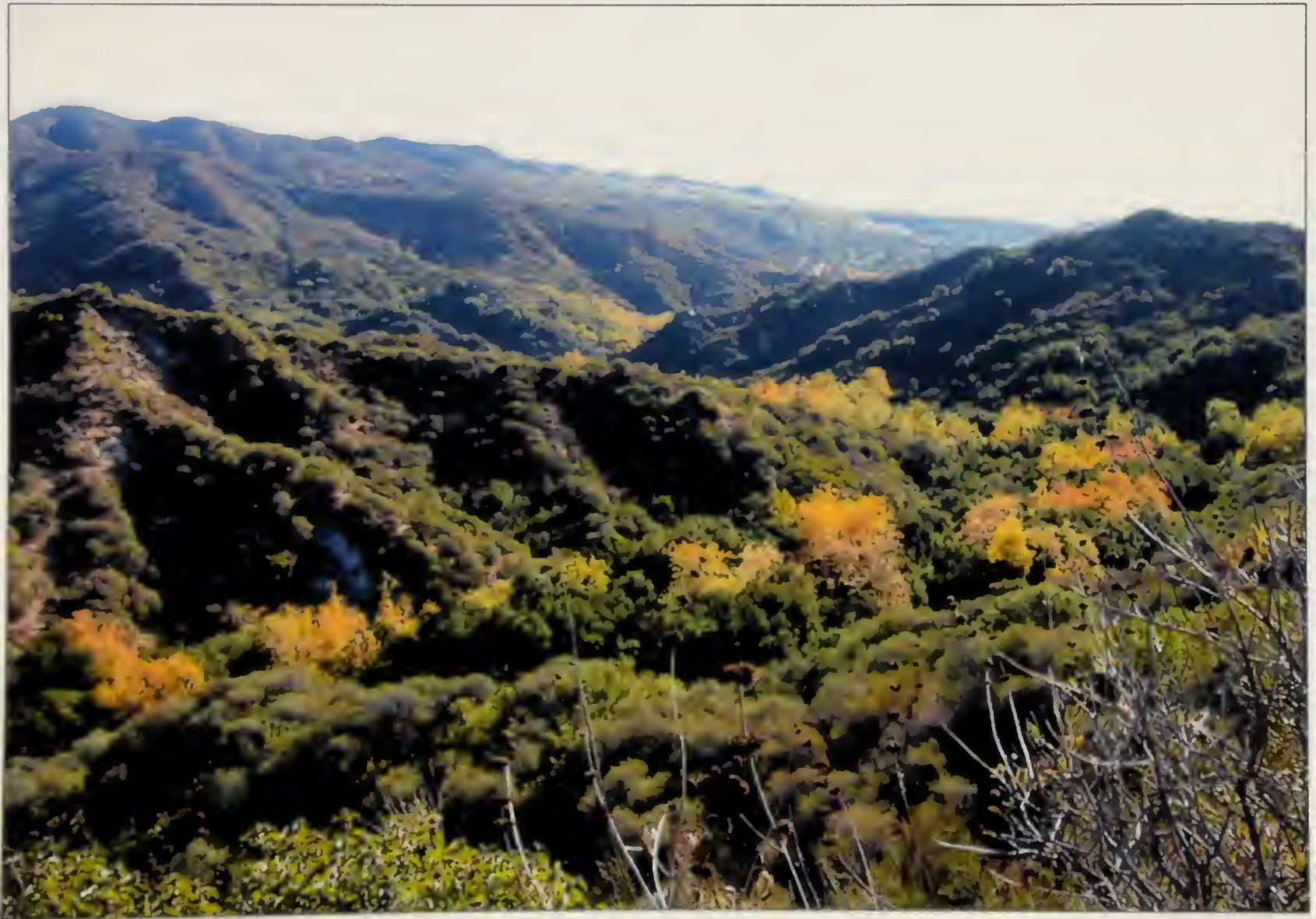

Figure 1c. Chaparral with oak riparian corridor. Note housing development in the distance.

ranchers and more recently to the movie industry. The Santa Monica Mountains serve as a backdrop or location for countless movies and television shows. The ecological and recreational values of the mountains have been widely recognized and much of the land is protected as county, state and federal parkland within the Santa Monica Mountains National Recreation Area. This paper presents an introduction to the biogeography of the Santa Monica Mountains, a summary of their cultural history, and a brief overview of preservation challenges.

DISCUSSION

The Santa Monica Mountains, together with the four northern Channel Islands, form the southwestern-most portion of a series of east-west trending mountains that make up the Transverse Ranges of Southern California. The Santa Monicas are a low range from 5 to 21 km wide, extending from the Oxnard plain approximately 70 km east to the Los Angeles River. They are bordered by the Pacific Ocean and the Los Angeles Basin on the south, and the San Fernando Valley and the Simi Hills on the north (Figure 2).

The Santa Monica Mountains are small but rugged, with elevations varying from sea level to 948 m at Sandstone Peak near the western end of the range. The crest of the range and the long ridges that extend southward toward the coast from this crest are generally 450-600 m in elevation. Streams that drain the south face of the range generally flow in deeply incised canyons, while the northern flank of the range is drained by short steep canyons that descend to the San Fernando and Conejo Valleys at about 300 m elevation. The only exception to this pattern of drainage is antecedent Malibu Creek, which originates in the Simi Hills to the north and cuts through the range to Santa Monica Bay in the south. Major streams flow year-round, at least at a subsurface level, but with greatly reduced volumes during the summer drought period. There are no natural lakes, but streams, springs, and seeps are common.

Geology

The geologic structure of the Santa Monica Mountains is that of a broad anticline, pushed upward and uplifted beginning about 3 million years ago in response to pressures from the interactions between the Pacific and North American Plates. The process of mountain uplifting, which continues today, has been accompanied by the formation of fault planes, the most notable of these being the Malibu Coast Fault that runs along the southern margin of the range.

The oldest rocks of the Santa Monica Mountains are slates exposed at the eastern end of the range above Pacific Palisades. These slates were originally formed as shales when mud was deposited on the floor of a shallow ocean during the Cretaceous period (144 to 65 mybp) and later metamorphosed into slate as plutonic granitic rock pushed up from the mantle. Approximately 25 to 10 million years ago a shallow ocean basin again covered the region, depositing thick beds of sandstones and shales. Major volcanic activity during this period led to basalt flows and breccias, particularly in the western half of the range where there are extensive extrusive volcanic formations.

Most of the summits along the crest of the Santa Monica Mountains are somewhat flattened, apparently remnants of a Cenozoic erosion surface reduced to low relief prior to the most recent uplift events (Dibblee 1982).

The Simi Hills (Figure 3) are geologically distinct, but closely related low mountains laying parallel and north of the Santa Monica Mountains, connecting to the Santa Monica Mountains proper through a series of hills west of Calabasas. They are generally considered part of the Santa

Figure 2. General land and topographic relief in the Santa Monica Mountains area.

Figure 3. The Simi Hills several months after the 2005 Topanga Fire.

Monica Mountains ecoregion and are included in the Santa Monica Mountains National Recreation Area. They form a northeast-trending ridge of approximately 24 km in length between the San Fernando Valley and the Oxnard Plain and separate the San Fernando Valley on the southeast from Simi Valley on the north. The Simi Hills are eroded from resistant, thick-bedded sandstone strata dipping north and have an average elevation of about 600 m over their length.

Climate

The Santa Monica Mountains, like all of southern California, have a Mediterranean-type climate characterized by mild, wet winters and hot, dry summers. During the summer, a marine layer of fog is common along the coast during the morning hours, but dissipates by early afternoon (Figure 4). Inland valleys may be fog-shrouded early in the morning, but as temperatures increase the fog dissipates until it crests the mountains and is vaporized or pushed out to sea. The coastal zone is classified as *Mediterranean cool summer with fog* in the Köppen system of climate classification, defined as areas with more than 30 days per year of dense fog. Inland of the coastal fog belt the climate is *Mediterranean warm summer* where the average temperature of the warmest month exceeds 22°C.

Figure 4. View of the Santa Monica Mountains with the marine fog layer that is common during the summer months.

While the mean annual precipitation at the base of the Santa Monica Mountains in west Los Angeles is about 440 mm, slightly higher than that in downtown Los Angeles, rainfall in wetter years around the base of the mountains is commonly 600-700 mm (Huffman 1998). Mean annual rainfall along the Malibu coast of the range is about 300 mm. Higher areas of the mountains receive about 625 mm in an average year, and received as much as 1,500 mm in the wet winter of 2004-05. On average, 86% of the Santa Monica Mountains' rainfall occurs between November and March, with the majority (47%), concentrated in January and February, falling in large storms that last for several days. The dry season typically extends from May through October. Significant rainfall during the summer months of June, July and August is a rare event. Evaporation generally exceeds precipitation from April to November (Keeley 2000).

The most significant feature of the regional rainfall pattern in addition to its unusual seasonal distribution is its high degree of variability and unpredictability. Long periods may occur between storms in a single season, and enormous variation exists among total rainfall amounts between years. At the UCLA weather station, the lowest rainfall year (1990, 130 mm) is approximately one third the normal annual mean of 430 mm, while the highest rainfall year (1984, 1040 mm) is almost 250% of the normal annual mean. Multiple years of low rainfall and extended drought punctuated by moderate to extremely wet years are not uncommon. Additional variation in rainfall pattern occurs with respect to geographic location.

December through March are the coolest months and July through October the hottest months in the Santa Monica Mountains. Along the immediate coast both winter and summer temperature extremes are moderated, but as one moves inland to the interior canyons and valleys, temperatures become higher in summer and lower in winter. Mean monthly maximum summer temperatures can vary 10-20 °C between UCLA at the base of the mountains on the coastal side and Canoga Park on the inland valley side (Raven et al. 1986). Winter night temperatures average as much as 10°C colder four km inland from the immediate coast (Boorse et al. 1998). Coastal sites rarely freeze, while inland sites often experience freezing nights between December-February with lows down to –8°C (Boorse et al. 1998). The frequency and duration of freezing events in the Santa Monica Mountains have been shown to affect chaparral species' distributions and plant dieback (Boorse et al. 1998, Langan et al. 1997).

Wind speeds vary in intensity and duration throughout the year within and adjacent to the Santa Monica Mountains. During summer days airflow is generally directed inland from the west, southwest, south and southeast. At night, airflow patterns reverse and travel toward the ocean. The Santa Monica Mountains periodically experience extreme foehn-type winds locally called Santa Ana winds. These winds result from a regional, large-scale weather pattern caused by the atmospheric pressure differential between a Great Basin high-pressure cell and a Pacific Coast trough of low pressure. Santa Ana winds average 30-50 km hr^{-1} and maximum gusts over 160 km hr^{-1} have been recorded. In the Santa Monica Mountains these winds are funneled through the north-south canyons and are therefore predominantly north or northeasterly winds. Relative humidity levels at the coast may be well below 10% under these conditions.

Santa Ana winds have been identified as the primary drivers of the wildfire regime in southern and central California shrublands (Moritz, 1997, Keeley and Fotheringham 2001). Although Santa Ana winds can occur in any month, they predominate from September to December. The major fires in the Santa Monica Mountains coincide with this peak of Santa Ana activity when vegetation is dry and temperatures high. A second small peak of Santa Ana wind activity occurs in March, but this is usually a time of cool temperatures and high moisture and does not create the severe fire conditions that occur during the fall Santa Ana winds.

Vegetation

Although the Santa Monica Mountains and Simi Hills are surrounded by a heavily urbanized environment, most of these ranges remain covered by natural or semi-natural vegetation with only about 13% of the area occupied by urban or suburban development (Figure 5). The distribution and composition of plant communities are determined mainly by the amount and seasonality of available water, temperature conditions, and light. These factors, in turn, are influenced by elevation, aspect, slope, soil type, proximity to the ocean, and fire history (Rundel and Gustafson 2005). The history of local human land use is also a significant factor. Extensive cattle ranching was carried out in many parts of the area in the 19th and early 20th centuries.

Several approaches to classifying plant assemblages in the Santa Monica Mountains have been published. Munz (1959) identified seven plant communities: coastal strand, coastal salt marsh, freshwater marsh, coastal sage scrub, chaparral, valley grassland, and southern oak woodland. Raven et al. (1986) in the *Flora of the Santa Monica Mountains* used much the same categories, adding riparian woodland and several wetland habitats.

More recently, Franklin (1997) developed a vegetation map of the Santa Monica Mountains that identified 12 communities (Figure 5), which are derived from 26 vegetation associations identified by the California Natural Diversity Database classification system (Holland 1986). The most recent classification, based on the Manual of California Vegetation (Sawyer and Keeler-Wolf 1995) and field sampling of over 3,900 stands of vegetation, defined 84 vegetation alliances or unique stands and 204 associations or phases (Keeler-Wolf et al. 2006, plus see this volume).

Shrublands
Chaparral is the major vegetation type in the Santa Monica Mountains and Simi Hills (>54% total vegetated area, based on Franklin 1997), generally occurring above 300 m on steep mountain slopes, but in some areas extending to lower elevations. Most of this is characterized as northern-mixed chaparral with *Ceanothus* species as dominants or co-dominants. Chamise and redshank (*Adenostoma*) chaparral occur only infrequently (< 3% total vegetated area). The second most common vegetation type is coastal sage scrub (~20% total vegetated area). It occurs on drier sites and lower elevations than chaparral, especially on coastal, south-facing slopes of the Santa Monica Mountains and on inland areas of the Simi Hills (Rundel 2007). Characteristic plants include black and purple sage (*Salvia mellifera* and *S. leucophylla*), California sagebrush (*Artemisia californica*), coast goldenbush (*Isocoma menziesii*) and ashy- leaf buckwheat (*Eriogonum cinereum*). The ubiquitous laurel sumac (*Malosma laurina*) is often emergent in this type, where it is able to extend its root systems deep into vertical strata layers to tap groundwater pools. The coastal sage scrub community, generally occurring on shallow soils and in recently eroded areas, plays an important role in soil stabilization.

One of the characteristic elements of chaparral and coastal sage vegetation of the Santa Monica Mountains, and an important contributor to their floristic diversity, is the abundant growth of a post-fire ephemeral flora that occurs in the first one to three years following fire. Annual herbs comprise more than three-fourths of the total post-fire species richness, areal cover, and biomass. Some of these annuals are fire-following specialists, which persist in inter-fire years only in the seed bank. Other species, while more abundant following fire, may persist in canopy gaps, on disturbed sites, or at xeric margins.
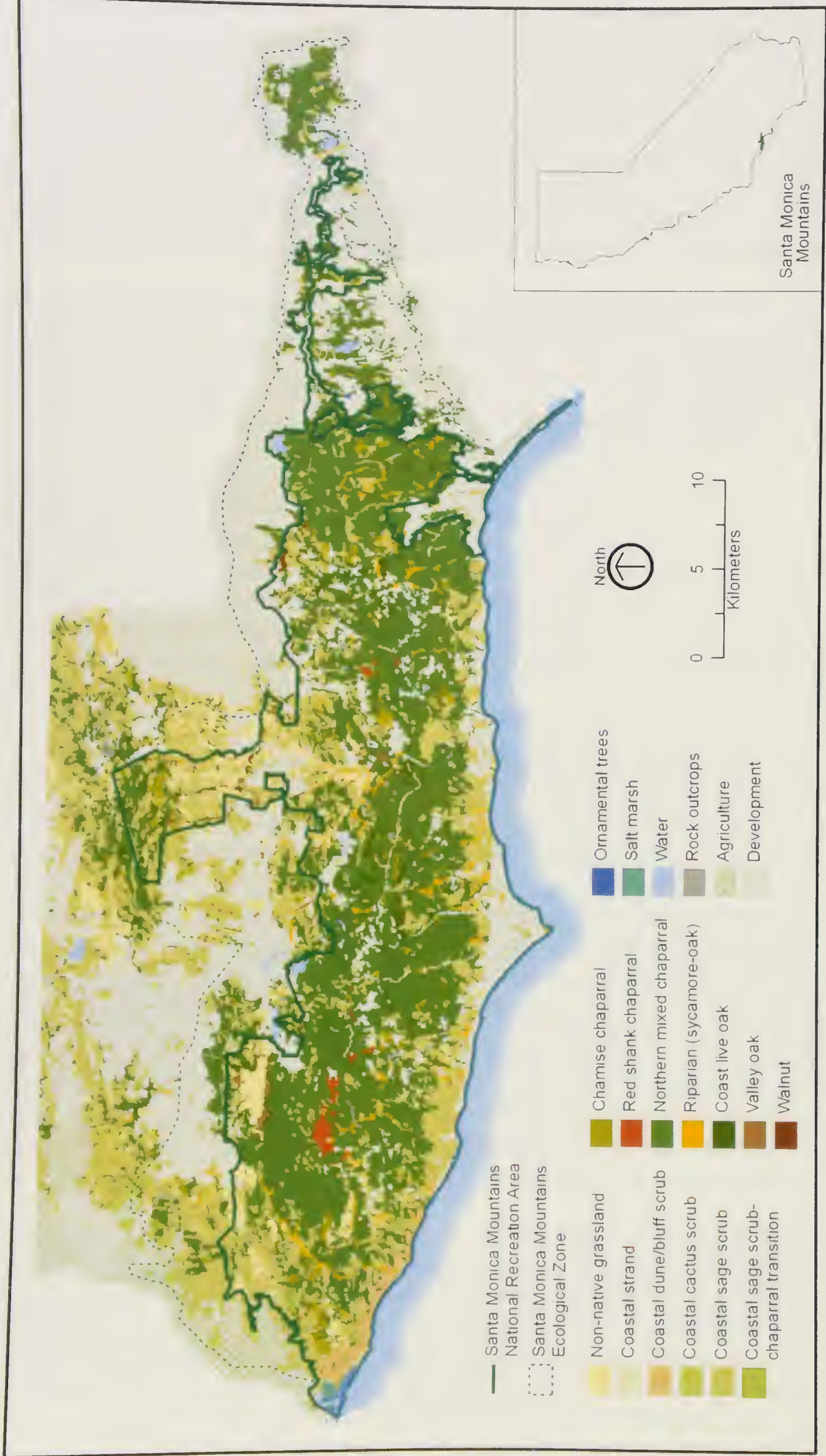
Figure 5. Vegetation and cover types of the Santa Monica Mountains and Simi Hills (Franklin 1997).

Santa Monica Mountains
National Recreation Area

Santa Monica Mountains
Ecological Zone

Non-native grassland
Coastal strand
Coastal dune/bluff scrub
Coastal cactus scrub
Coastal sage scrub
Coastal sage scrub-
chaparral transition

Chamise chaparral
Red shank chaparral
Northern mixed chaparral
Riparian (sycamore-oak)
Coast live oak
Valley oak
Walnut

Ornamental trees
Salt marsh
Water
Rock outcrops
Agriculture
Development

North

0   5   10
Kilometers

Santa Monica
Mountains

Woodlands

Coast live oak woodland (3% of total vegetated area), characterized by coast live oak (*Quercus agrifolia*), is found on more mesic sites on north slopes, in shaded ravines, canyon bottoms and along streams. Coast live oak woodland can vary from a mostly closed canopy to a more open canopy on drier sites, often with a rich understory of vines, herbaceous perennials and shrubs. Frequent associates include hollyleaf redberry (*Rhamnus ilicifolia*), California bay laurel (*Umbellularia californica*), coffeeberry (*Rhamnus californica*) and poison oak (*Toxicodendron diversilobum*). When coast live oak woodland occurs along stream courses in conjunction with riparian tree species it is considered to be riparian woodland. It also intergrades with northern mixed chaparral on north-facing slopes, while *Q. agrifolia* can form an oak savanna with scattered individuals in grassland. Live oaks are evergreen with deep taproots that can reach to the water table.

Riparian woodland (1.7% of total area) occurs along canyon and valley bottoms with perennial or intermittent streams in nutrient rich soils, or within the drainages of steep slopes. The riparian community has high plant species diversity (Rundel and Sturmer, 1998). Dominant species are coast live oak (*Quercus agrifolia*) and sycamore (*Platanus racemosa*) while associated or locally dominant species include arroyo willow (*Salix lasiolepsis*), black willow (*Salix laevigata*), alder (*Alnus rhombifolia*), California black walnut (*Juglans californica*), Mexican elderberry (*Sambucus mexicana*), California bay laurel (*Umbellularia californica*) and mule fat (*Baccharis salicifolia*). Riparian woodland is a particularly important plant community because of its limited area, critical resources for animal populations, role in geomorphic stabilization, and its high biodiversity.

California walnut woodland with *Juglans californica* (0.2% of total area) is most commonly found on the north-facing slopes of the Santa Monica Mountains and in small stands in the Simi Hills on deep soils with high clay content (Quinn 1990). Walnut woodlands in the Santa Monica Mountains can occur with an annual grassland, native herbaceous, or coastal sage scrub understory, or intermixed with north slope chaparral and oak woodland. Springs or subsurface water availability are generally present in these sites.

Valley oak savanna, also called valley oak woodland (0.7% of total vegetated area), is typically a grassland savanna with widely spaced *Quercus lobata*. In the Santa Monica Mountains coast live oak (*Q. agrifolia*) can grow with valley oak on hillside areas. Tree density may increase along bottomland riparian corridors where valley oaks are an important component of the riparian woodland. Valley oaks, which reach their southernmost extension in the Santa Monica Mountains, are not especially drought tolerant and need deep soils with available soil moisture for growth (Meyer, 2001). Typically, valley oaks in this community cover less than 10% of the ground area, with annual grasslands dominating the matrix below. Characteristic grasses include widespread alien species such as wild oats (*Avena fatua*), ripgut brome (*Bromus diandrus*), and black mustard (*Brassica nigra*), as well as remnant stands of native purple needlegrass (*Nassella pulchra*). Native wildflowers include a diverse assemblage of geophytes, in particular mariposa lilies (*Calochortus catalinae*) and blue dicks (*Dichelostemma capitatum*).

Grasslands and Coastal Habitats

Valley grassland and non-native annual grassland (4% of total vegetated area) in the Santa Monica Mountains are dominated by oats (*Avena* spp.) and ripgut brome (*Bromus diandrus*). Within the non-native annual grasslands, isolated stands of native grasses exist consisting primarily of purple needle grass (*Nassella pulchra*) and, to a lesser extent, foothill needlegrass (*Nassella lepida*). Native forbs are infrequent within the annual grasslands. On burning, the

grasslands generally go to mustards (*Brassica nigra* and *Hirshfeldia incana*) for several seasons before returning to annual grassland. The mustard seedbank appears to be long-lived, persisting through 10 or more years without burning. Most of the larger annual grasslands in the Santa Monica Mountains and Simi Hills have a history of grazing and agricultural use.

Salt Marsh
Coastal salt marsh (0.3% of total area) occurs in estuaries where semi-enclosed coastal waters have a free or periodic connection with the open ocean. The major areas of this community are at Malibu Lagoon and Point Mugu lagoon. Because stream flow is so low in summer, these areas are lagoons rather than estuaries for much of the year. Plants in this community adapt to high concentrations of salt by either using succulence to allow storage of salts in vacuoles or having salt glands to excrete excess salts. Characteristic plants are pickleweed (*Salicornia* spp.), marsh jaumea (*Jaumea carnosa*), salt grass (*Distichlis spicata*), and sea blite (*Sueda californica*). From Santa Barbara to the border with Mexico, approximately 75-90% of the original salt marsh habitat is estimated to have been lost (Zedler 1982). The isolation, rarity, and small extent of coastal salt marsh habitat make this community especially important in the Santa Monica Mountains.

Coastal Dunes, Terraces and Bluffs
Coastal communities (0.5%) occur on sand along the immediate coast. Much of this community has been lost to development or recreational uses. The habitat is characterized by strong winds, salt spray, fog, intense solar radiation, drought conditions and an infertile, unstable substrate (sand). It extends from above the high tide zone landward in a narrow band along the southwestern edge of the mountains east of Point Mugu. Characteristic dune plants include sand verbena (*Abronia umbellata*), silver beachweed (*Ambrosia chamissonis*), saltbush (*Atriplex leucophylla*), beach morning glory (*Calystegia soldanella*) and the alien iceplant or hottentot fig (*Carpobrotus edulis*).

Wildlife

The Santa Monica Mountains and Simi Hills support an abundant diversity of wildlife, which is reflective of the diversity of the vegetation. More than 450 vertebrate species have been reported, including 50 mammal, 384 bird (113 breeding bird), and 36 reptile and amphibian species. The relatively intact wildlife populations of the mountains are especially impressive considering their proximity to one of the largest urban areas in the United States. The continued maintenance of wildlife populations in the Santa Monica Mountains is dependent on the ability of public and private land managers to ensure adequate habitat for the most sensitive species. As urban development within the mountains climbs up canyons, expands in pockets of low lying land, tops ridges, and encroaches on habitat adjacent to protected public land, it continues to remove and fragment habitat available to wildlife.

Occupation by Native Peoples

The Santa Monica Mountains have been at the center of complex human interactions for thousands of years. Archeological site density in the Santa Monica Mountains is very high, with more than 1,000 known archeological sites representing pre-contact and historic native occupations.

At the time of historic European contact, the Santa Monica Mountains were occupied by Native Americans of two tribal affiliations, the Chumash and Gabrielino/Tongva (King 2000). The

Chumash held much of the south-central California coast, including the northern Channel Islands, as well as inland portions of the Coast and Peninsular ranges. Archeological and linguistic data suggest that the Chumash culture may have evolved in place for more than 9,000 years. The western and central Santa Monica Mountains comprised the southernmost extent of Chumash settlement. The Chumash population at the time of contact is estimated to have been in the range of 15,000 to 20,000 people, perhaps 1,300 of whom resided in the Santa Monica Mountains region. Historical records document at least six coastal and 10 interior Chumash villages in the Santa Monica Mountains region. Village populations ranged from perhaps 15 to 400 individuals, and coastal villages were, on average, somewhat larger than those of the interior. Each village had associated resource extraction sites in its respective territory, often distinctive from their living areas.

At historic contact, the Chumash did not practice traditional agriculture, living rather as hunter-gatherers on the great diversity of plant, animal and insect life found in the region. Villages along the coast were particularly adept at the extraction of marine resources, including dozens of fish species, marine mammals, and a variety of molluscs. Terrestrial animals utilized included large mammals (deer and pronghorn), small mammals, reptiles and various birds. Plant foods assumed particular significance among the Chumash, with geophyte bulbs, roots of yucca, small seeds, acorns and other nuts, fruits, and greens being the chief staples. The Chumash had extensive knowledge of the seasonal availability of plant foods, and were able to harvest virtually year-round. Although not traditional agriculturalists, the Chumash engaged in a variety of resource management activities, of which fire was the most important. Intentional burning was conducted in order to spur the growth of desired plant species, facilitate hunting, reduce fuel loads, and for many other purposes. It appears, however, that the Chumash did not burn extensively in the Santa Monica Mountains and that most vegetation conversion around villages may have instead been a result of fuel gathering.

At European contact, the territory of the Gabrieleno/Tongva encompassed the Los Angeles Basin and portions of the adjacent mountain ranges and the southern Channel Islands, including the easternmost Santa Monica Mountains. The Gabrieleno/Tongva residing in the Santa Monica Mountains were members of a distinct Western Tongva group, whose territory also included the southern San Fernando Valley, southern Channel Islands, downtown Los Angeles and San Pedro. On the basis of archeological and other evidence, the Gabrieleno/Tongva appear to have arrived in the region between 2,500 and 3,000 years ago. Nine historic Western Tongva villages have been identified in the Santa Monica Mountains region. Most of these villages were located in the interior, and populations ranged from about 10 to 360 inhabitants. Subsistence practices among the Gabrieleno/Tongva were similar to those of the Chumash, with extensive utilization of both marine and terrestrial resources.

Euro-American History

The Spanish Era
Sporadic Spanish contact with the Santa Monica Mountains began in the 1500s with exploratory voyages along the Pacific coast. The first Euro-American accounts of the Santa Monica Mountains came from the explorations of the Spaniard Juan Cabrillo, who anchored in the small bay of Malibu Lagoon in October 1542, claimed the land for the King of Spain and named it "Pueblo de las Canoas" (Town of the Canoes), because of the many impressive Chumash canoes which came to his ships to greet him. Nevertheless, a sustained Spanish presence in the region

was not established until the late 1700s. Three Franciscan Missions—San Gabriel (founded in 1771), San Buenaventura (founded in 1782) and San Fernando (founded in 1797)—and the Los Angeles Pueblo (established in 1781) were the important economic and social centers in the region. With the mission era, agricultural lands were cleared and cattle and sheep ranching became a major land use.

In an effort to strengthen its hold on Alta California, Spain offered land grants to private citizens for economic development. These ranged from hundreds to many thousands of acres in size. Seventeen such grants were established within and adjacent to the Santa Monica Mountains, most of which served as cattle ranches (or ranchos). Local Native Americans were quick to relocate to ranchos and find employment as cowboys or vaqueros; abandonment of several native villages in the Santa Monica Mountains between 1770 and 1800 (prior to Mission recruitment) might be attributable to this phenomenon.

The Mexican Era

When Mexico won its independence from Spain in 1821, Mexican officials and land speculators pressed for distribution of mission property. During the 1820s and 1830s, the Mexican government passed legislation to both diminish the influence of the Franciscans and distribute mission lands to settlers, and by 1834 all of the mission lands were secularized and opened to occupation. In addition, the Mexican government continued the Spanish practice, begun decades earlier, of granting private individuals large tracts of land.

California Statehood

In 1850, California was admitted to the Union and Los Angeles began to take form as a city. Congress passed the California Land Act in 1851, establishing a three-person Land Claims Commission and a complex legal mechanism to determine the legitimacy of Hispanic land claims. The indefinite boundaries of the unsurveyed landholdings, the lack of documentation in the possession of the claimants, and both the expenses of the legal fees and the time necessary to establish title in the courts often delayed confirmation of landholdings, sometimes for decades. In addition, title to the former rancho concessions was frequently clouded by the host of American newcomers who, taking advantage of a process burdened with confusion and delay, simply settled on the land and were later looked upon favorably by the non-Hispanic courts.

By the 1870s, the demand for land in California prompted the subdivision of many of the larger landholdings, although cattle ranching continued. Since the latter decades of the 19th century, the rapid subdivision and re-subdivision of land, often punctuated by claims and counter-claims, has been an enduring characteristic of much of the California landscape, including pockets of the Santa Monica Mountains.

The rapid post-war expansion of Los Angeles brought increased recognition of the ecological and recreational value of the Santa Monica Mountains. Governments began to purchase parklands in the 1960's and 1970's and in 1978, in response to a grassroots movement, Congress established the Santa Monica Mountains National Recreation Area with the intent to preserve the area's scenic, natural and historic setting.

Land Preservation

Today the boundary of the Recreation Area includes 61,000 hectares in the Santa Monica Mountains and Simi Hills. Approximately 30,000 hectares are protected as local, state and federal

parks, including Topanga, Malibu, Leo Carillo and Mugu State Parks, Ahmanson Ranch (Mountains Recreation and Conservation Authority), Cold Creek Canyon (Mountains Restoration Trust), Circle X Ranch, Zuma Canyon and Cheeseboro/Palo Comado Canyons (National Park Service). Although parkland continues to be acquired, it is intended that much of the Recreation Area remain private lands. This creates a complicated intermix of developed and natural areas within the mountains that, with the impinging pressures and environmental changes resulting from surrounding urbanization, present challenges for the protection and management of these valuable natural areas. Following is a brief discussion of some challenges both common to southern California and particular to the Santa Monica Mountains.

Management Challenges

The coastal and foothill regions of Southern California form a critical area within California contributing to the state's designation as one of the select group of 25 global biodiversity *hotspots.* Whether one measures biodiversity in terms of numbers of plant and animal species present or by conservation significance as measured by numbers of designated rare and endangered species, coastal Southern California rates higher than any other part of California or the continental United States (Rundel 2002). It is here in Southern California that the influences of the Mediterranean-climate regime combine with a diverse topography and dynamic fire cycles to produce mosaics of a wide variety of habitat types including the chaparral, oak woodlands and savannas, coastal sage shrub, grasslands, riparian woodlands, wetlands, and coastal marshes found in the Santa Monica Mountains.

Both the spatial and temporal scales of habitat occurrence and dynamics have been critical factors in the evolution of our biodiversity. Remarkably, this biodiversity exists adjacent to the second largest urban center in the nation. As our urban core expands and suburban outlying areas are developed, enormous threats to biodiversity arise. Six of the ten counties in the continental United States with the largest numbers of threatened and endangered plant and animal species are in California, including San Diego, Los Angeles, San Bernardino, and Santa Barbara Counties (Rundel 2002).

Threats to biodiversity in the Santa Monica Mountains and all of California are real. We know of at least 21 animal species and 34 plant species that have become extinct in recent decades. Another 17 animal species once common in California have been extirpated from the state, although they survive elsewhere. These include charismatic species such as the California grizzly bear, our state animal which was once common in the Santa Monica Mountains, as well as the gray wolf. Nearly two-thirds of California's native fish species are extinct, endangered or in significant decline.

Many parts of the Santa Monica Mountains exist as islands of natural habitat within an urban sea. The existence of this habitat and open space with dramatic views so close to (indeed, within) the Los Angeles metropolitan area makes the mountains especially desirable to many in the region who are seeking a less-urbanized lifestyle. In recent years development on private lands has proceeded rapidly despite regulatory efforts by local governments. This increased development and urban encroachment have become major threats to ecological viability across the region through their impact on habitat fragmentation and loss of connectivity. The impacts of habitat fragmentation on wildlife are many and varied and can profoundly affect the ability of remaining wildlands to support wildlife populations (Wilcox 1980, Shaffer 1981, Simberloff and Abele 1982).

Increased fire frequency associated with human activities can have a significant impact on vegetation structure. Although the plant communities of the Santa Monica Mountains are tolerant

of wildfire and resilient to a relatively wide variation in the fire return interval, chaparral and coastal sage scrub communities can be degraded by high fire frequencies with a short fire return interval (Keeley and Fotheringham 2003). Where fires are frequent, non-native herbaceous annual vegetation has been observed to increase and replace shrublands (Vogl 1977, Barro and Conard 1987, Haidinger and Keeley 1993, Beyers et al. 1994). This type conversion of shrubland to annual grassland has been widely observed throughout southern California (Keeley 1990, Keeler-Wolf 1995, Minnich and Dezzani 1998).

In human-dominated, fragmented landscapes, frequent fires near fragment edges may facilitate the invasion of edge-associated non-native plants and animals into natural areas. The openings and disturbed areas created after fires can accelerate invasions by disturbance-associated exotic plants, increase the entry of development-associated animal species into natural areas, and facilitate other types of human-caused habitat alteration due to the proliferation of social trails and off-road vehicle access routes (Sauvajot et al. 1998). This combination of frequent human-caused fires and disturbance-facilitated impact invasions along the urban-wildland interface may significantly alter the distribution and abundance of native wildlife in fragmented systems.

Large fires can also exacerbate the problems caused by habitat fragmentation. Fire can act as an extirpation mechanism, leading to the local disappearance of certain species from a burned area (Sauvajot 1995). In pristine systems, the long-term population impacts of such extinction events may be inconsequential because of the availability of nearby unburned habitat to serve as a recolonization source. However, if fire-induced extinctions occur in fragmented habitats, local populations may be eliminated entirely if the burn encompasses the entire habitat fragment. In addition, because local population sizes are already relatively small in habitat fragments, fire-associated mortality may actually push population levels below viability thresholds for some species. If the affected fragment is not close enough to recolonization sources, local extinctions can be permanent. Increased studies of metapopulation dynamics in the Santa Monica Mountains would provide important data for better understanding these impacts of habitat fragmentation.

CONCLUSIONS

The Santa Monica Mountains are a unique, biologically diverse natural preserve within the second most highly populated urban area in the nation. The Mountains also have a rich cultural heritage, beginning with their occupation by native peoples and extending to their present popularity as a filming location for the movie industry. The ecological, cultural and recreational values of the mountains have been widely recognized and, at the behest of the public, large areas as parkland have been protected by city, county, state and federal agencies and private organizations. These groups continue to acquire parkland or otherwise protect land through conservation and trails easements, with several large and ecologically significant additions made only within the last few years. However, much of the Santa Monica Mountains remain, and will remain, in private ownership while the area surrounding the mountains continues to develop and increase in population.

The internal ecological threats that may arise from development of private lands within the range and the exogenous threats that arise from the heavily populated areas surrounding the Santa Monica Mountains cannot be managed only through the acquisition of selected lands and administration of conservation easements. Many, if not most, of the decisions and actions that affect natural resource conservation in Santa Monica Mountains are made by private individuals and the many local government agencies that have jurisdiction around and within the mountains.

Effective programs for the management of natural ecosystems and protection of biodiversity in the Santa Monica Mountains must in the future rely not just on public park and conservation agencies, but on private/public partnerships as well. Proactive planning processes involving all of the stakeholders in the Santa Monicas will be the key to successful preservation and sustainability of our natural systems.

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THE SANTA MONICA MOUNTAINS IN A GLOBAL CONTEXT

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ABSTRACT: The Santa Monica Mountains lie within the "biodiversity hotspot" of the California floristic region, and present a globally significant example of the classic mediterranean-climate evergreen shrublands. The five regions of the world with a mediterranean-climate regime include only about 2.25% of the world's land area but contain nearly 50,000 plant species. This diversity per unit land area, as well as the ongoing threats to their sustainability, makes these ecosystems more significant for biodiversity in many respects than tropical rainforests. The patterns and processes that have led to the evolution of this biodiversity are not well understood. An approach to understanding biodiversity is made by comparing species richness in the Santa Monica Mountains with two small ranges with similar size and elevation in other mediterranean-climate regions where plant diversity is higher – the Stirling Range in southwestern Australia and the Cape Peninsula in South Africa. Serious threats of habitat fragmentation and transformation are present in all three areas.

KEYWORDS: Mediterranean, biodiversity, shrublands, Stirling Range, Cape Peninsula

The Santa Monica Mountains represent one of the best examples of mediterranean-climate ecosystems in California, with relatively intact and protected examples of evergreen chaparral, coastal sage scrub, woodlands, and riparian habitats. The global significance of mediterranean climate ecosystems has been recognized in recent years because of their remarkable plant species richness proportional to their small area (Cowling et al. 1996b, Rundel 2007; Table 1). This diversity has led to designation of the five Mediterranean biomes by international conservation groups as global *biodiversity hotspots*, defined on the basis of their high levels of plant endemism and high levels of human disturbance (Mittermeier et al. 2005). Animal species richness is moderately high but less notable than the plant diversity. The global significance of Mediterranean-climate ecosystems makes management and preservation of biodiversity of these areas a critical need.

Mediterranean-Climate Regions

Five regions of the world share a mediterranean-climate regime – California, central Chile, the Mediterranean Basin, the Cape Region of South Africa, and southwestern and South Australia (Figure 1). These regions are characterized by warm, dry summers and mild, rainy winters; unusual in that the great majority of the earth's surface experiences either summer or year-round rainfall regimes brought on by either continentality and the monsoon effect or a year-round rainfall regime in coastal areas. This unique climatic regime is associated with the widespread

Table 1. Comparative species richness of native vascular plants and major vertebrate groups for the five mediterranean-type climate regions of the world. Some caution must be used in interpreting these numbers because of varying contexts of what constitutes core mediterranean-climate habitats. These data come from the Conservation International "hotspot" descriptions of the five MTEs (Mittermeier et al. 2005, www.biodiversityhotspots.org).

	Vascular plant species	Mammal species	Bird species	Reptile species	Amphibian species	Fish species
California*	3,488	160	350	54	69	73
Chile **	3,529	64	226	87	43	216
Mediterranean Basin	22,500	224	497	228	77	43
Cape Region	8,550	127	324	100	51	34
Southwestern Australia	5,571	57	285	177	33	20

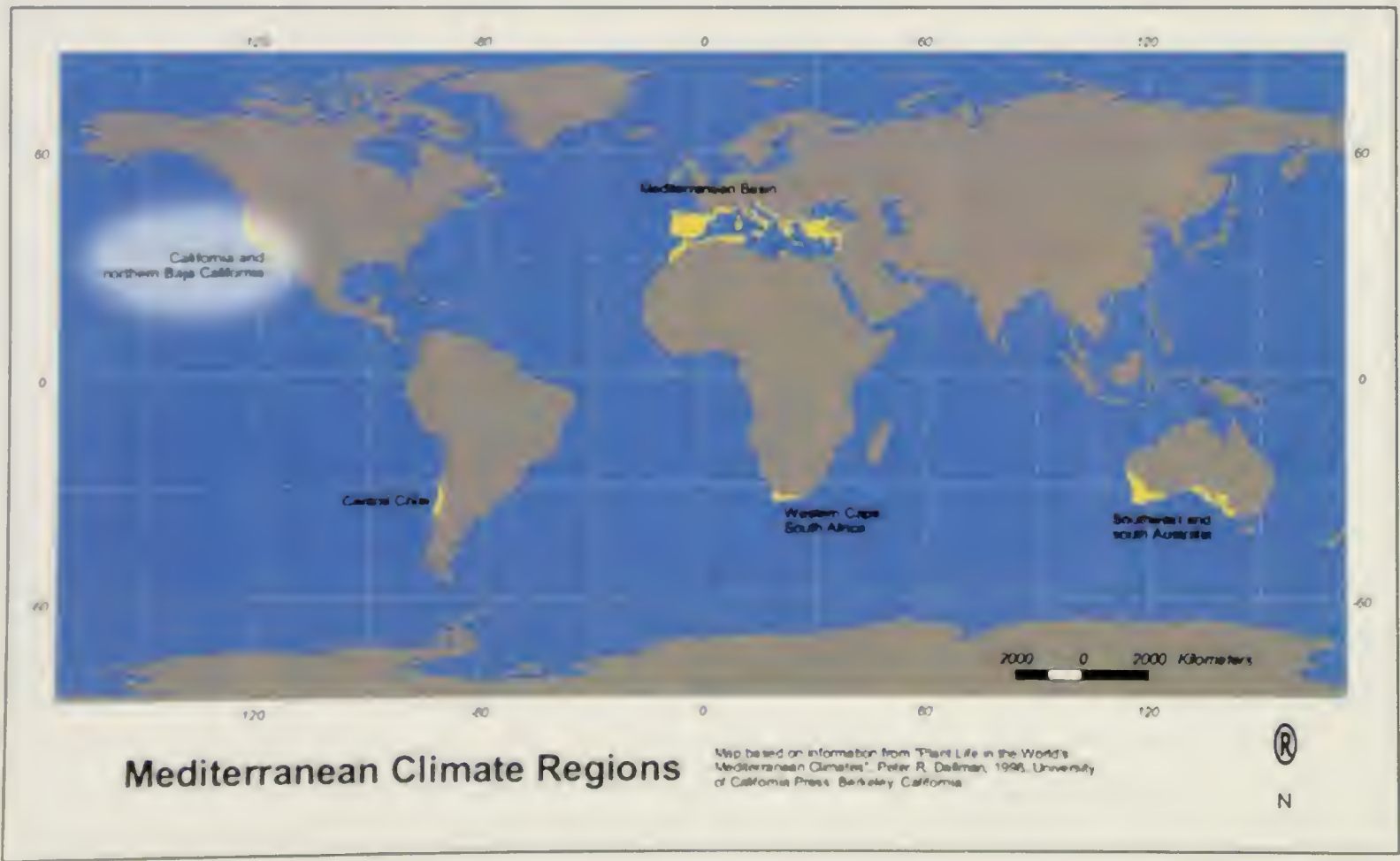*   excl. deserts

** "hotspot" Chile

Figure 1. The geographic distribution of the five regions of the world with a mediterranean-type climate regime.

dominance of evergreen shrublands (Cowling et al 1996b, Rundel 2007).

The characteristic plant association in mediterranean-climate regions is an evergreen, leathery-leaved shrubland, and this growth form has been a major focus of comparative studies among and between regions. Despite a structural similarity in this shrubland community in all five regions, the contemporary flora of each region comprises an admixture of floras independently derived from relict subtropical forest as well as recently evolved drought- and fire-adapted lineages. Before the onset of global cooling and aridification in the Pliocene, subtropical forests dominated all five regions. Sclerophyllous vegetation and dry woodlands subsequently replaced these forests, most prominently during the Quaternary, when the strongly seasonal mediterranean-type climate developed. At the same time, fire became a significant factor in all regions except Chile, although contemporary natural fire regimes vary regionally.

Global Significance of Mediterranean-Type Ecosystems

On the basis of land area, the five mediterranean regions collectively form only about 2.25% of world land area (Figure 2). This area is not equally distributed among the regions but lies largely in the Mediterranean Basin, which comprises over 70% of this total area. California, central Chile, and southwestern Australia have mediterranean-climate regions of similar size, while the Cape Region of South Africa is the smallest of the regions. Despite this small global spatial extent, the five mediterranean-climate regions possess remarkably large vascular plant floras (Table 1). The richest of these regions is the Mediterranean Basin, with an estimated 25,000 plant species. The small Cape Region contributes over 9,000 species. Accepting recent estimates that the global diversity of vascular plants is approximately 300,000 species, the five mediterranean-climate regions contribute 16% of the global total (Figure 2). Proportional to their area, this is a far greater diversity than that of the tropical rainforests, yet the levels of human disturbance and threats to biodiversity in these regions are extremely great (Rundel et al. 1998, Rundel 1999, 2007).

Despite decades of research and the international recognition of the global significance of mediterranean-climate regions, we still have an imperfect understanding of the historical, climatic and biotic factors responsible for the evolution and maintenance of this high level of species richness. Patterns of plant species richness with land area are significantly different among the five regions. A log-log plot of species richness versus area for four of the five regions demonstrates this pattern (Figure 3). The Cape Region has significantly higher species richness at all scales of area, while Southwestern Australia is notably high at landscape areas of 10-100 km, and at regional levels. California has intermediate levels of richness at all spatial scales.

A Tale of Three Ranges

A useful approach to understanding the causal patterns of biodiversity in mediterranean-climate regions is to examine comparable landscape areas between regions. The geomorphology, climate, and area of the Santa Monica Mountains make them an interesting case study for comparison with two ranges of similar area and landforms – the Stirling Range in southwestern Australia and the Cape Peninsula extending south from the city of Cape Town in South Africa (Table 2).
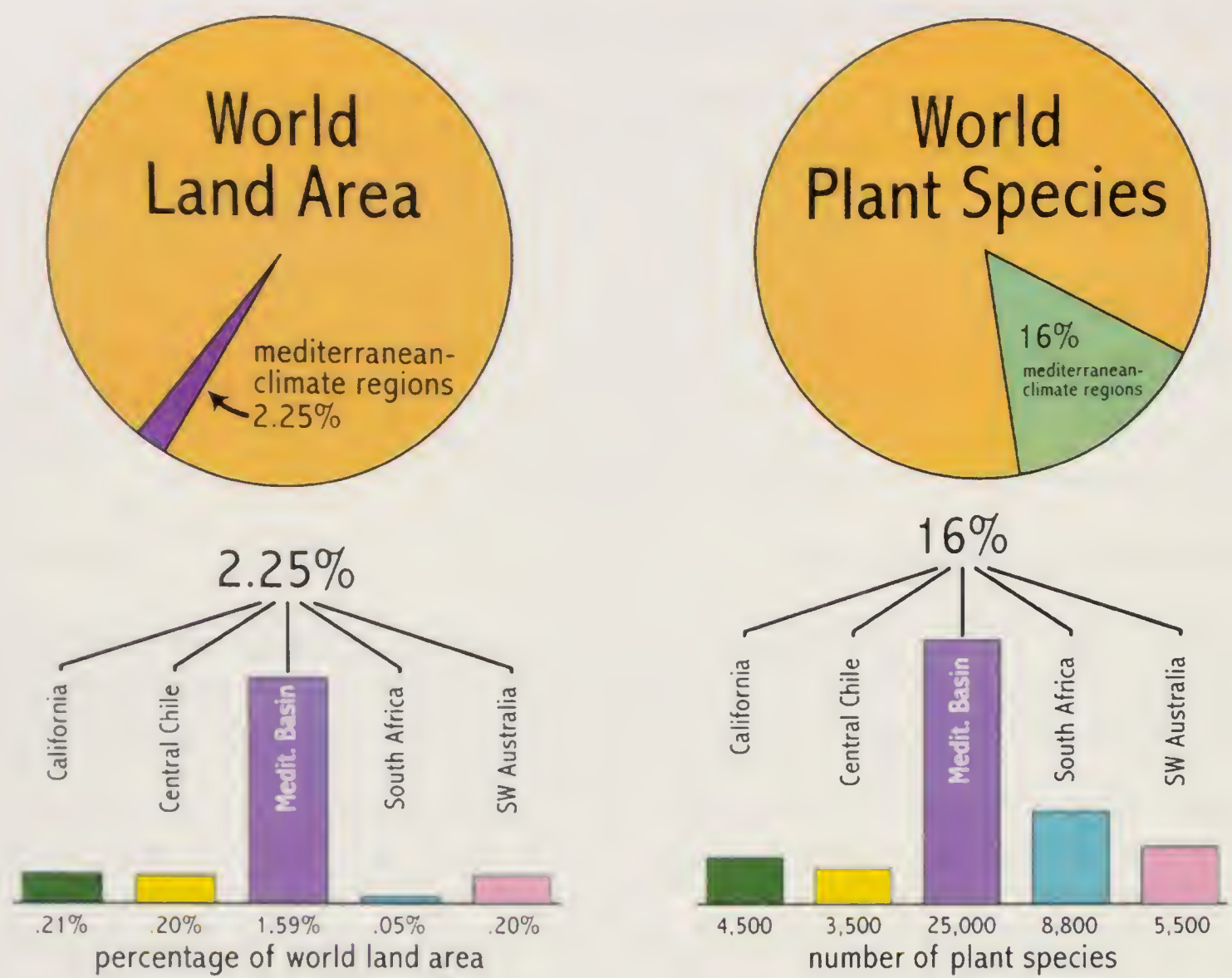
Figure 2. Absolute and relative areas of the land area and vascular plant species richness of the five mediterranean-climate regions in comparison to global land area and species richness. Plant species richness assumes the existence of 300,00 vascular plant species. Drawing by Lisa Pompelli.
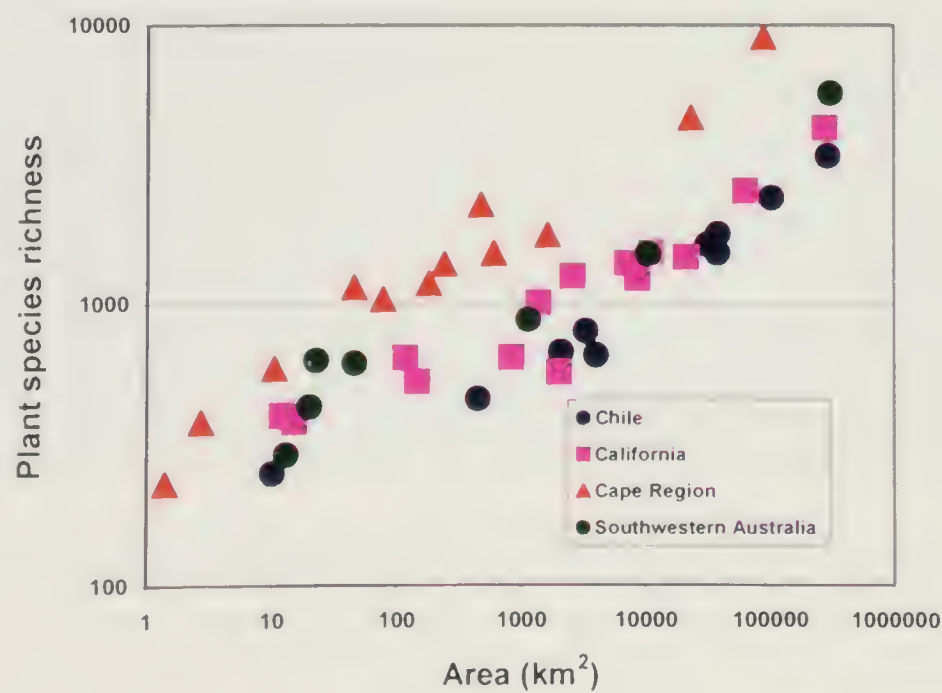
Figure 3. Vascular plant species richness in relation to area for four mediterranean-climate regions. Data from Cowling et al. (1996b), Hobbs (1992), and Arroyo et al. (1994).

Table 2. Comparative geography and biodiversity of the Santa Monica Mountains/Simi Hills, the Stirling Range, and the Cape Peninsula. Data from NPS records, Raven et al. 1986, Thompson et al. 1993, Cowling et al. 1996a, Trinders-Smith et al. 1996, and Picker and Samways 1996).

|	Santa Monica Mtns. California	Stirling Range SW Australia	Cape Peninsula South Africa
Area (km2)	985 (SMM flora)	1156	471
Maximum elevation (m)	948	1073	1113
Rainfall (mm yr-1)	300 - 700	400 - >700	400 - 2270
Mammal species	41	35	41
Breeding bird species	113	90	155
Reptile species	22	33	48
Amphibian species	8	14	18
Vascular plant species	894	1530	2285
Vascular plant endemism	2 species	87 species	90 species
Largest genera	*Lupinus* -13	*Eucalyptus* - 52	*Erica* - 103
	Phacelia - 12	*Stylidium* - 39	*Aspalathus* - 55
	Lotus - 11	*Melaleuca* - 30	*Senecio* - 47
	Trifolium - 10	*Leucopogon* - 28	*Ficinia* - 37
	Camissonia 10	*Acacia* - 28	*Oxalis* - 28
Largest families	Asteraceae - 107	Myrtaceae - 160	Asteraceae - 286
	Fabaceae - 46	Proteaceae - 144	Iridaceae - 168
	Poaceae 44	Fabaceae - 141	Fabaceae - 162
	Scrophulariaceae - 33	Orchidaceae - 123	Cyperaceae - 146
	Cyperaceae - 23	Asteraceae - 92	Poaceae - 141
			Orchidaceae - 118
Five largest families/total flora	36%	43%	45%

The Santa Monica Mountains of the Transverse Ranges of coastal southern California are a low range from 5 to 21 km wide extending from the Oxnard plain to the Los Angeles River, approximately 70 km to the east. They cover approximately 985 km^2, bordered by the Pacific Ocean and the Los Angeles basin on the south and the San Fernando and Conejo Valleys and the Simi Hills on the north. The highest region is in the west, reaching 948 m at Sandstone Peak. Rainfall varies from an average of 300 mm along the coast to about 700 mm at the highest elevations. In wet years rainfall can be as much as 700 mm at low elevations and 1500 mm at high elevations. The Santa Monica Mountains are described in detail in an earlier paper in this volume.

The Stirling Range lies in the southwestern area of Western Australia, approximately 340 km southeast of Perth, where it extends over 60 km in width from west to east (Thompson et al. 1993, Olver and Olver 1998; Figures 4 and 5). The highest point in the range is Bluff Knoll, which reaches 1,095 m elevation. It is the tallest peak for a thousand kilometers or more in any direction
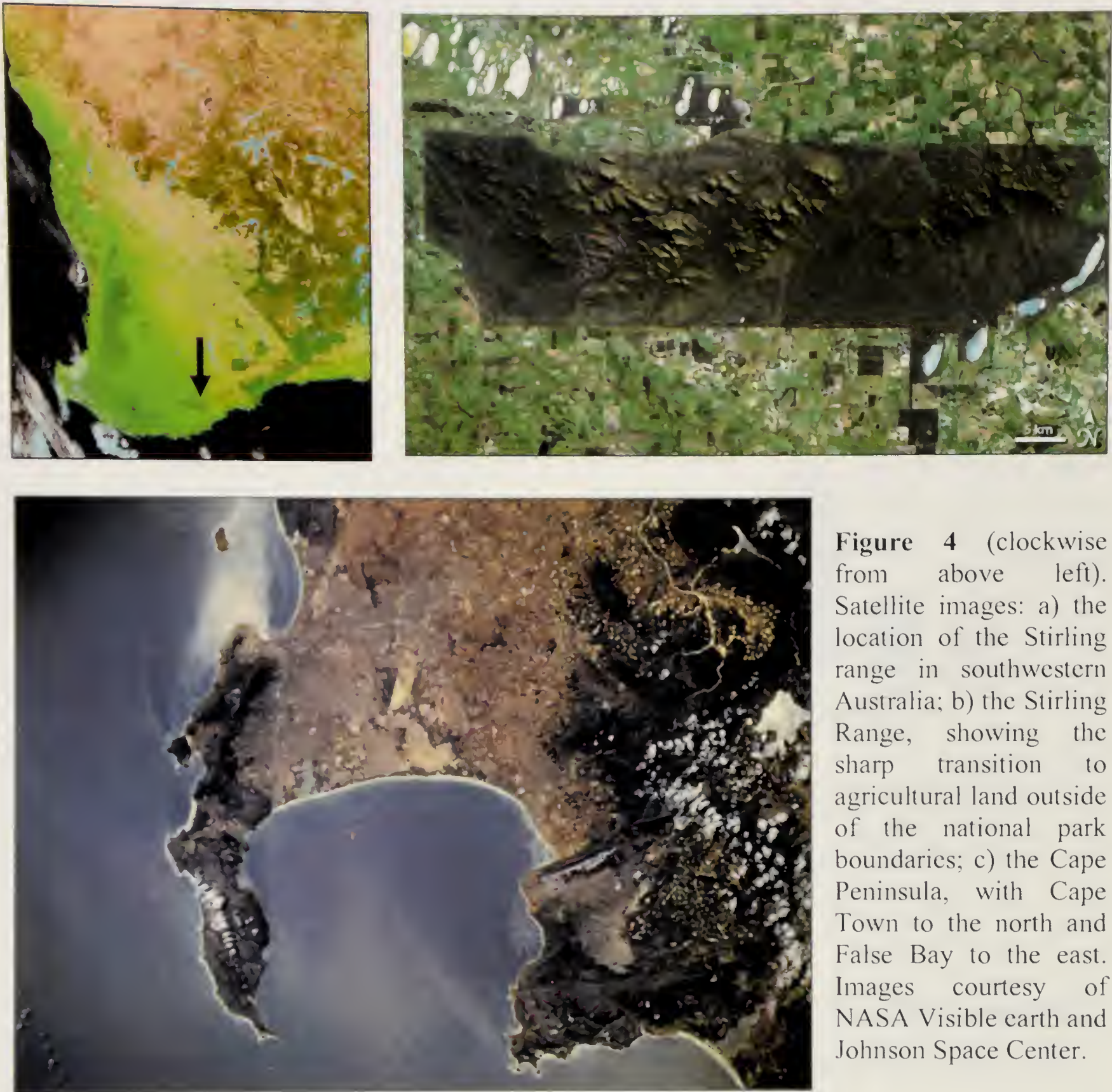
Figure 4 (clockwise from above left). Satellite images: a) the location of the Stirling range in southwestern Australia; b) the Stirling Range, showing the sharp transition to agricultural land outside of the national park boundaries; c) the Cape Peninsula, with Cape Town to the north and False Bay to the east. Images courtesy of NASA Visible earth and Johnson Space Center.

and the only point in Western Australia to receive regular winter snowfall. Mean annual rainfall in the Stirling Range is quite comparable to that of the Santa Monica Mountains away from the immediate coast, varying from a low of 400 mm at lower elevations to somewhat above 700 mm on the highest peaks. The range covers 1,179 km^2, making it very close in area to the Santa Monica Mountains and Simi Hills.

The Cape Peninsula extends from the city of Cape Town south along the Table Mountain Chain to Cape Point in the south where it forms the southwestern point of the African continent (Cowling et al. 1996a, Pauw and Johnson 1999, Wolfart 2001; Figure 6). The peninsula separates the Atlantic Ocean to the west from the Indian Ocean to the east. Its notable landscape features include the famous Table Mountain, which reaches an elevation of 1,113 m, and the Cape of Good Hope. Covering 471 km^2, the Cape Peninsula has slightly less than half of the area of the Santa Monica Mountains.

Figure 5. The Stirling Range, southwestern Australia (clockwise, from top): a) general landscape; b) heathland vegetation; c) *Kingia australis* (Dasypogonaceae). Photographs by Grant Wardell-Johnson.
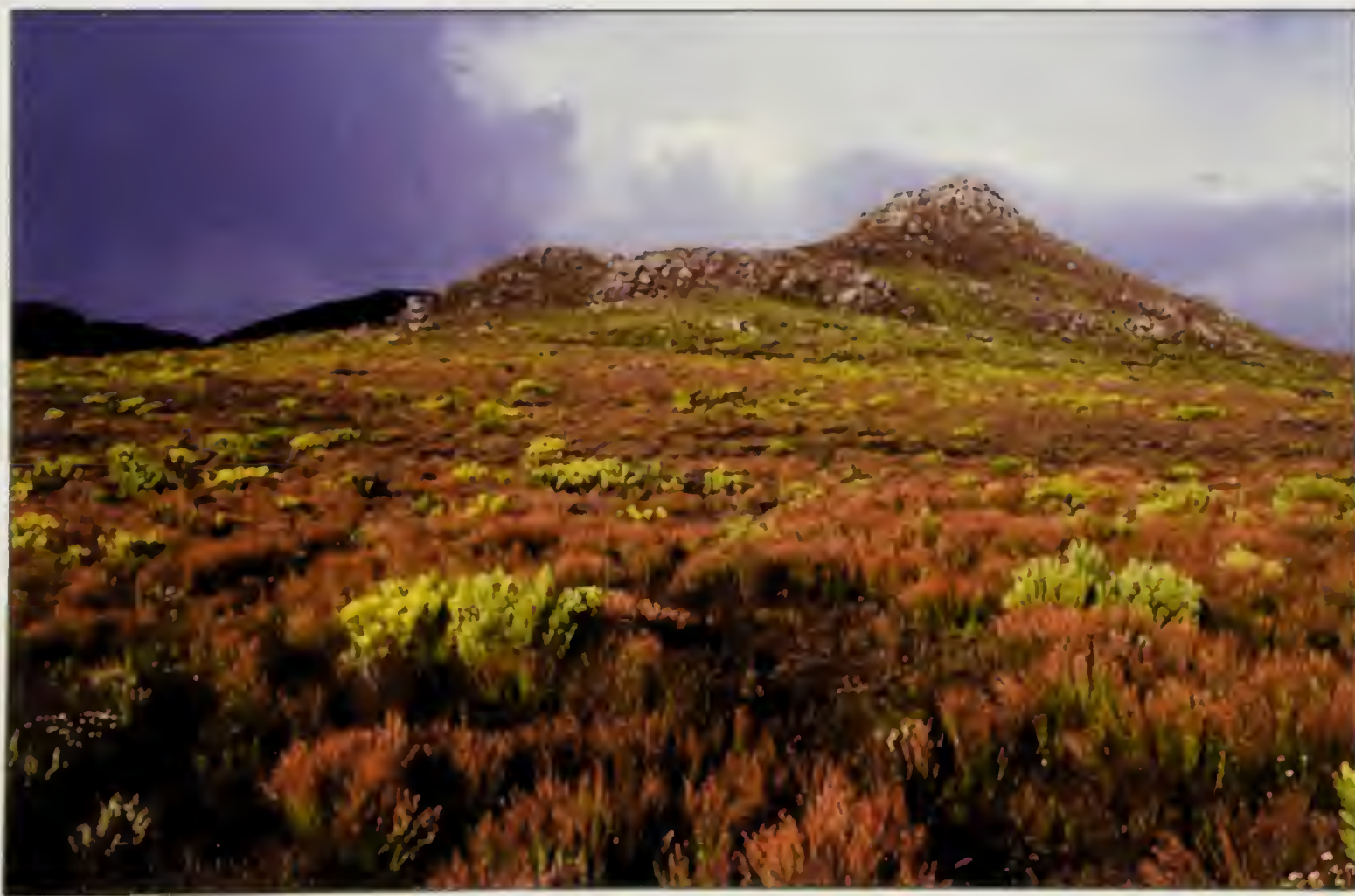
Figure 6. Cape Peninsula, South Africa (clockwise from top): a) Table Mountain and the city of Cape Town, looking from the north; b) fynbos of *Elegia filacea* and *Leucodendron laureolum*; Photographs by Guy Midgley.

The maritime position between two ocean expanses gives the Cape Peninsula an unusual weather regime, with mean annual rainfall reaching 2,270 mm on Table Mountain. As with the Santa Monica Mountains National Recreation Area, Table Mountain National Park lies adjacent to a large metropolis, and for this reason is fragmented by urban development and privately owned land. It receives more than four million visitors annually.

The biodiversity of vertebrates among the three ranges is surprisingly similar (Table 2). Comparing extant native species, the Santa Monica Mountains have mammal species richness as high or higher than the other regions. Certainly both the Cape Peninsula and Stirling Range have lost many mammal species in historical times, but we similarly had mass extinctions of mammal species at the end of the Pleistocene. Our diversity of breeding bird species is intermediate between those of the Cape Peninsula and Stirling Range, while we rank poorly in comparison in the number of reptile and amphibian species present. High species richness of reptiles in the Stirling Range relates in part to reptile species utilizing niches normally filled by mammal species in other regions.

The most intriguing comparisons come with respect to vascular plant species (Table 2). The Santa Monica Mountains' native flora of 894 vascular plant species is far eclipsed by the 1,530 species present in the similar area of the Stirling Range (Thompson 1993) and the remarkable 2,285 species known from the Cape Peninsula in an area only half as large (Kidd 2004, Trinder-Smith 2006). We have no simple explanation for this differential pattern of plant diversity, but there is increasing evidence linking climate history, fire regime, and rainfall reliability (Cowling et al. 2005).

At the plant family level, there are similar patterns of relative diversity among the three ranges (Table 2). The five largest families comprise a similar 36-45% of the total floras. The Asteraceae and Fabaceae are among the five largest families in each of the regions, while the Poaceae and Cyperaceae reach this level in both the Santa Monica Mountains and Cape Peninsula. These family similarities tell only part of the story, however. There is a striking difference in the growth forms represented in the largest families and genera of the Santa Monica Mountains compared to the other two ranges. Our largest genera are almost entirely represented by annuals and herbaceous perennials, and speciation has not produced extensive adaptive radiation within our region. By comparison, many of the large genera are woody shrubs and/or trees in the Stirling Range and shrubs in the Cape Peninsula.

Adaptive radiation is notable in these two ranges, as in their broader regions, in the number and the very large size of many genera. *Erica*, for example, has more than one hundred species present in the small area of the Cape Peninsula, while there are 52 species of *Eucalyptus* present in the Stirling Range. We lack woody genera with large numbers of species.

Comparative rates of endemism demonstrate that gamma diversity in plant communities is clearly high in both southwestern Australia and the Cape Region of South Africa. Only two plant species are endemic to the Santa Monica Mountains, and both of these have likely reached this status as the result of extirpation in other parts of their range. In comparison, the Stirling Range and Cape Peninsula have 87 and 90 endemic species, respectively (Table 2).

Conservation is a major issue in all three ranges. Table Mountain National Park, like the Santa Monica Mountains National Recreation Area, includes large areas of protected habitat, but with major fragmentation associated with private lands and a location adjacent to a major urban center. Although the Stirling Range is relatively isolated from major urban areas and entirely protected as

a national park, it lacks any buffer zone of natural area to separate it from agricultural and grazing lands (Figure 4a).

CONCLUSIONS

Mediterranean-type ecosystems have provided many opportunities for comparative studies of the controlling factors in the evolution of biodiversity. These five regions share common characteristics of climatic regime, with an independent evolution of plant and animal species adapted to these conditions within each region, and thus provide a natural ecosystem experiment with five independent replications. Beyond the broad regional comparisons that have been made, it is valuable to compare smaller areas of comparable landscape forms, as in the three small ranges described here. The value of comparative studies between these ranges lies not only with their mediterranean-climate similarities, but with subtle differences in climatic conditions, ecosystem dynamics, evolutionary history, and human impacts that have led to the patterns of diversity that we see today. The large numbers of rare and endangered species in these regions gives a special significance to expanding studies to better understand the evolution of diversity and adaptive radiation that mediterranean-type ecosystems exhibit. Serious threats of habitat transformation and degradation in all of these areas make it critical that there be a better understanding of conservation biology and sustainable resource management.

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RESEARCHING A NEW FLORA OF THE SANTA MONICA MOUNTAINS AND SIMI HILLS, CALIFORNIA

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ABSTRACT: A new flora for the Santa Monica Mountains and Simi Hills is being researched and written, to replace a flora that was last published in 1986. At least 1,150 taxa are now known to occur within the range. The purpose of the new version is to make identification easier for all users. All species descriptions are being done from living materials and are as complete and precise as possible using all parts of the plants. Once published in 2009, the entire flora will be placed online with color images, the herbarium database, and dichotomous keys and polyclaves to make it possible for positive identification by any user.

KEYWORDS: Santa Monica Mountains, Simi Hills, flora, polyclaves

DISCUSSION

In 2000 the UCLA Herbarium began a project to produce a new vascular plant flora of the Santa Monica Mountains (SMM) and Simi Hills (SH), to replace the aging flora of the Santa Monicas by Raven, Thompson, and Prigge (1986). The SMM extend from Griffith Park and the Hollywood Hills in Los Angeles County, skirted by the Los Angeles River on the north, westward to Calleguas Creek near Camarillo (77 km), and south to the Pacific Ocean at the Point Mugu Naval Air Station in Ventura County. These mountains create the uphill southern edge of the San Fernando Valley. The many communities within the SMM include Brentwood, Bel Air, Beverly Hills, Hollywood, Pacific Palisades, Malibu, Topanga, Calabasas, Agoura Hills, Westlake Village, and Thousand Oaks. As defined, the SMM now exclude the densely populated flat areas in the city of Santa Monica and the San Fernando Valley.

The Simi Hills extend from northern Chatsworth in Los Angeles County westward, and contact the SMM at Arroyo Canyon near Thousand Oaks in Ventura County. Communities included in the SH, at least in part, are Chatsworth, Chatsworth Manor Lake, the fringes of West Hills, Hidden Hills, and the currently undeveloped slopes of Oak Park, Thousand Oaks, and Newbury Park. The goal of the flora project is to describe all species reproducing without supplemental watering within the defined area which, excluding all developed sites, covers 900–950 km^2. Our working title for the project is *A Naturalist's Flora of the Santa Monica Mountains and Simi Hills, California*. It is scheduled for publication in 2009.

The floristic project is still in a stage of description and discovery, so that numbers of taxa occurring within the range are progressively changing or can be expected to change before publication. The current working list includes 1,100 species of ca. 530 genera plus at least 50 additional subspecies and varieties, and thus equals one-seventh of the state total (Hickman 1993). This list has increased from 880 species in 440 genera and about 900 total taxa reported in Raven et al. (1986). From that total, species known only from West Los Angeles or Santa Monica

were excluded At least 40 genera with horticultural species that have successfully become established in the region will be included in the new flora.

Numerous genera of non-natives have been added by researchers and consultants working in the SMM range since the last flora, but also at least 15 genera are new to the range as well as interesting native species such as *Centaurium exaltatum*, *Nicotiana clevelandii*, and *Piperia elongata.*Systematic studies since 1986 have also led to the alteration of generic names for species, especially as taxonomic redefinitions have appeared in *Flora of North America*. To date, inclusion of the Simi Hills has only added about 30 species to the list, and nearly all SH discoveries have been noteworthy natives. This flora will set a new baseline for occurrence of native, introduced, and invasive species, and becomes a benchmark for future studies on invasive species and conservation of native forms.

The flora still includes only one lycophyte (*Selaginella bigelovii*) and 20 species of ferns and horsetails (monilophytes), all native. At least one individual of the native *Juniperus californica*, a male plant of a dioecious species, still survives at Cornell Corners in Agoura Hills (SMM). Several cultivated species of conifers will be included in the new flora because they have become established from seeds along roads, but fortunately none has shown a tendency to become invasive.

To date collectors have discovered at least 760 taxa of angiosperms native to the range, which is very close to the predicted value for a mainland California landscape based on a native species-area plot and regression line (Raven et al. 1986). Monocotyledons currently comprise 18.5% of the total flora and 210 ± 10 taxa (Poaceae = 60%). Species of non-grass monocot families are nearly always native (ca. 88%), whereas native species of Poaceae are substantially less frequent (ca. 38%) and many are hardly ever seen or collected. The ten species of introduced monocot species belonging to non-grass families are generally unnoticed in the flora, although *Washingtonia robusta* appears to be exhibiting invasive tendencies, and certain species of *Cyperus*, while not invasive at this time, have that potential. The remaining angiosperms (eudicots, magnoliids, water lilies) comprise 78.5% of currently known taxa, of which approximately two-thirds are native. One-third of the taxa in the new flora belong to three plant families: Asteraceae, Poaceae, and Fabaceae. Eleven percent of all taxa are from the ten largest genera: *Atriplex*, *Bromus*, *Camissonia*, *Dudleya*, *Eriogonum*, *Juncus*, *Lotus*, *Lupinus*, *Phacelia*, and *Trifolium*. Three-quarters of the genera are represented in the flora by only one or two species.

The new version of the flora will be exceptional among modern floras because our technique is to describe plants directly from fresh, local materials and not to depend, as is traditional, on flattened, browned herbarium materials for descriptions. It is our estimation that most local users attempt to identify plants when they are living, i.e., green, and in flower, and descriptions and keys for identifying plants need to highlight conspicuous and diagnostic features that are often obscured when specimens are dried (e.g., color, 3-D shapes, surface features, and smell) in addition to traditional taxonomic characters. It is our goal to write newly researched, full descriptions of every taxon rather than to copy published descriptions that are highly abbreviated, and have not taken into account variations, especially in size, observed in some of our local populations.

What is also unusual about the UCLA project is that both authors do every species together, rather than subdividing the taxa. A species is collected in the wild, and then the fresh samples are used immediately to create a first draft description (Gibson). An effort is made to sample different individuals so as to find the typical form, the largest and the smallest sizes and variants in the

color and texture of parts. Since April 2003, approximately 840 taxa have been described. This first draft description rarely includes fruits and seeds, which must be collected and described and appended weeks or months later when they are mature. The second draft (Prigge) occurs on another day or even in a different month or year, using additional fresh materials and reconsidering and judging again every observation and measurement and utilizing all references, databases, and past herbarium collections. Since 2004, approximately 430 second drafts have been completed. Discrepancies between the two descriptions and observations of past authors are then thoroughly discussed, in order to determine what research is needed to clarify or complete the description to monographic quality. The second draft is then edited to conform to the same format for every species so that it can be sent out for review by a specialist of that group. The review draft is generally at least three times longer, and hence much more detailed, than descriptions in current California floras for the region, e.g., *The Jepson Manual* (Hickman 1993). To date, 165 are ready for review. In addition, while botanizing in the SMM range we have been keeping track of every encountered species that is flowering; with an updated database on flowering times, we will be able to eventually report on flowering for 36 equal time periods throughout the year, and we will be able to say when and where a person could expect to see flowers of each species.

The new version of the flora has been developed using a set of guiding principles that have emerged while working with the public and environmental consultants over the last three decades, as follows:

(1) As much as possible, scientists need to produce floras that eliminate the need for the public to consult with and rely upon herbarium taxonomists. Not only are taxonomists becoming an endangered species in most academic institutions, but also they cannot on a regular basis be expected to identify plant materials. Theoretically, it should be possible to take the identification of difficult groups out of the hands of specialists and enable field researchers and learned amateurs to make dependable determinations on their own, even for species and subspecies belonging to "difficult" groups. Plant identification has created a perennial dependency on professional taxonomists by users who cannot master families and genera with small or non-showy reproductive structures or interpret subtle distinctions between sister taxa using technical characters. Online services now offer amateurs and professionals access to colored images, distributional and nomenclatural information, and some published descriptions, so that a user can access much of the information needed for a positive identification, but the non-showy taxa are still troublesome even using the most sophisticated information online.

(2) The public needs a flora that is a reasonable substitute for monographs of the past, which average users have no access to, and which will likely be less accessible in the future. What normally separates the success of a professional taxonomist from a learned user is not the ability to key plants out using a regional flora, but rather having herbarium specimens to examine and having access to old and thoroughly published treatments that no longer are available in most libraries. Conceivably, in time, this could be solved with an enormous investment in posting these resources online for all users. A person who does not have access to herbarium resources needs full descriptions of monographic quality. For "tough" groups even a professional botanist has a level of uncertainty after specimens are keyed out, because in many floras there are not enough distinguishing, reliable features to decide between forms that are superficially very similar. A strong indication that a given flora does not provide the complete tools for accurate identification is when a professional has to use multiple floras and monographs to identify a plant.

(3) At the outset, we decided to describe every part of the adult plant, so that every part becomes a possible feature for proper identification, and many differences can be given to distinguish closely similar forms. Seeds and fruits will be thoroughly described so that the flora can be used for diagnostic purposes in a variety of studies, including packrat midden research, analysis of animal stomach contents, and archaeological research. Descriptions often are helpful for bracts and bractlets, but rarely are they discussed except where heavily used for identification (e.g., spikelets of Poaceae or involucres of Asteraceae and Apiaceae). Glandular pubescence, when observed on fresh plants, may be obvious but becomes obscure on dried materials, thus resulting in confusion for the users. Flowers are sometimes not described well or at all for grasses in some floras, in which specialists have required identification primarily using fruiting materials.

(4) Scientists need to produce more reliable sets of dichotomous keys that utilize both vegetative and reproductive choices for crucial couplets. What is it about a plant that enables us to identify it to genus and species when we walk up to it in the field? Much of the practical knowledge of the naturalist is not generally employed in keys, but instead keys emphasize characters that can be used especially with dried herbarium materials. Vegetative characters can provide alternative characters to reproductive ones, which may not be present on the specimen. Moreover, local floras such as this one, with fewer species, give opportunities to easily separate species that on a statewide or regional basis may be technically difficult to identify.

In the standard hierarchical, dichotomous key required in every published flora, there is a set of either/or conditions, i.e., couplets or paired statements, that one follows in a sequential manner until the plant is identified. Dichotomous keys are not perfect, and often a key uses traits that are not present on the specimen being identified because of the time that the specimen was collected, e.g., fruit characters are needed but the specimen was in flower or only vegetative. In such cases, one has to proceed somewhat stochastically or work through the alternatives, a process that can lead to tentative and uncertain identifications. So, either a flora must have dichotomous keys that are infallible, or the user should have a way to get around such hazards and roadblocks. A computerized, digital identification process solves this problem, so for the new flora we plan to have two types of keys. The publication will have the traditional dichotomous keys, hopefully cleverly contrived to make it virtually impossible to fail. But because that ideal is likely not attainable, we plan to devise an online computerized program of polyclaves or multientry keys that solves, or at least minimizes, the problems of plant identification.

Polyclaves are nonsequential and permit a person to identify an organism by the characters that one has at hand. They were developed more than 50 years ago using either Keysort™ or computer punch cards (e.g., Hall and Johnston 1954; Hansen and Rahn 1969; Simpson and Janos 1974). Modern computer programs have made card identification systems virtually obsolete, and have added greater sophistication to the art of plant identification. The polyclave basically is a taxa × character matrix in which the taxa (e.g., family, genus, or species) can be selected or sorted by the characters selected, and thereby result in rapid identification. If you tell the program what characters that you have in front of you, the computer can give you a list of the species having all of those characters. Given more features, the computer can eliminate taxa that do not match the given character set and ultimately can suggest what species you have. There remains the problem of not having enough characters for proper identification; the specimen must supply enough useful characters. However, this process minimizes the common problem where "good" characters are not included in the key. It also avoids a common problem where an obvious, fairly diagnostic character is mentioned only near or at the end of a series of couplets; with the polyclave, such a character can be chosen at the start. Unlike dichotomous keys, which proceed

through an orderly sequence of characters from the first couplet to the last, polyclaves permit the entry of character states in any order, and they are able to sidestep problems of missing or difficult characters, which, for the frustrated user, seem to always occur in an early leg of a dichotomous key.

Some polyclaves have been made available by Meacham through UC Berkeley in the program MEKA version 3.00 (http://ucjeps.berkeley.edu/meacham/meka/). These include the Angiosperm Family polyclave, based on Hansen and Rahn (1969) adapted by Meacham and Duncan; and some California Asteraceae from treatments in *The Jepson Manual* adapted by Rosatti. Another program to be considered is the DELTA System (DEscription Language for TAxonomy) by Dallwitz (1980; Dallwitz, Paine, and Zurcher 1999) that now has numerous polyclave programs for interactive identification and information retrieval (Dallwitz 2005: http://delta-intkey.com/www/overview.htm).

For this flora with "only" 1,150 taxa, this should be a splendid test to determine whether an online polyclave can take over the burden of plant identification for an entire region. To do this, we expect to have more than 100 characters per species in the matrix. The website will also have thousands of color images to illustrate virtually every taxon and many technical features as they would be seen by an observer with no more than a simple hand lens (i.e., no electron photomicrographs or other high magnification illustrations). Also online will be an illustrated glossary for technical terms used in descriptions and keys, the full set of dichotomous keys, and access to the database of herbarium vouchers and sightings within range. Therefore, when this project is finished, it will consist of a printed flora of perhaps 800 pages, a simple, printed or printable manual having only the dichotomous keys for quick field use or use in classes, a set of CDs with the images, and a website including the polyclave program, the herbarium data base, and all of the published descriptions and illustrations. Having the flora online for the public will permit the list to be expanded and revised continuously as new species are discovered, more and better images are obtained, scientific names and authorities are changed, errors are found and corrected in descriptions and keys, specimens are added to the data base, etc. We envision a modern type of taxonomy class at local universities, where computers are an essential component not only teaching students where to search for digital color plant images, images of herbarium vouchers, nomenclatural and distributional websites, but also using polyclaves for local identification and obtaining complete descriptions.

CONCLUSION

Upon completion of *A Naturalist's Flora of the Santa Monica Mountains and Simi Hills, California*, we will have a modern flora for all taxa known in our area. While retaining the aspects of a traditional flora, with dichotomous keys and species accounts, the flora will also take advantage of information technology to make databases, digital images, and identification routines available on the Internet or on compact disks. Species accounts will be complete, thoroughly detailing the variation observed within our area, and the dichotomous keys will strive to be unambiguous by relying on well-differentiated vegetation and reproductive characters, especially features readily observed in fresh materials but obscured in pressed, dried specimens. A web site and compact disks will not only make the printed flora available in digital format, but also provide interactive routines (polyclaves) for plant identification and search routines to generate checklists for specific areas or species distribution maps. The flora, by its completeness and its database and identification routines, will free users from the need to rely on other floristic treatments, generic monographs, and the academic botanist to identify local plants.

One species you'll see in the upcoming flora: *Deinandra minthornii* (Jepson) B.G. Baldwin, the Santa Susana tarplant, is a subshrub listed as rare by the State of California. It grows along the edges of sandstone boulders in the Santa Monica Mountains and Simi Hills. Near Chatsworth in the easternmost Simi Hills, this species flowers during late fall and early winter with eight to 13 ray florets per head (above); in rainy years this species may also flower during summer months, with five to eight ray florets per head.

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AN ANNOTATED CHECKLIST OF THE LICHENS OF THE SANTA MONICA MOUNTAINS

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ABSTRACT: Two hundred ten taxa of lichens and lichenicolous fungi in 74 genera are reported from the Santa Monica Mountains. Seven lichens not collected since 1915 are discussed: *Acarospora schleicheri* (Ach.) A. Massal., *Catapyrenium squamellum* (Nyl. *ex* Hasse) J.W. Thomson, *Diploschistella athalloides* (Nyl.) Lücking, K. Knudsen & Fryday, *Lecidea cinerata* Zahlbr., *Micarea deminuta* Coppins, *Micarea erratica* (Körb.) Hertel, Rambold & Pietschm., and *Ramonia ablephora* (Nyl *ex* Hasse) R.C. Harris. *Buelliella inops* (Triebel & Rambold) Hafellner is reported from a new host, *Caloplaca bolacina* (Tuck.) Herre. *Lecanora subimmergens* Vain. and *Lecidea confluens* (Web.) Ach. are reported new to California.

KEYWORDS: Lichens, Santa Monica Mountains, Herman Hasse

INTRODUCTION

Herman Hasse (Figure 1) reported over 200 lichen species from the Santa Monica Mountains where he collected from around 1890 until his death in 1915 (Hasse 1898, 1913). This represents the most intensively collected area of southern California at a crucial time when urbanization began to irrevocably alter the Santa Monica Mountains, especially the south slope from Los Angeles to Santa Monica. The majority of Hasse's collections are at the New York Botanical Garden (NY) and Harvard at the Farlow Herbarium (FH) with important type collections in the Nylander Herbarium in Helsinki, Finland (H-NYL), and the Zahlbruckner herbarium in Austria (W). Due to different species concepts, it is not known exactly how many taxa recognized by lichenologists today Hasse actually collected in the Santa Monica Mountains. Many of these collections have been studied and revised by the lichenologists working on the Sonoran lichen flora project (Nash et. al. 2002, 2004, 2007; Tucker and Ryan 2006) though many problems require further study and can only be solved one at a time. The clarification of Hasse's legacy is necessary to establish a baseline for this region at the beginning of the 20th century. The importance of establishing the historical record is made clear by the fact that many taxa collected by Hasse, possibly as many as fifty, have not been collected in the Santa Monica Mountains since 1915, the year of his death. Seven species are discussed in this paper that have only been collected by Hasse, but even these species may be rediscovered.

The author is engaged in work on clarifying the historical record and hopes to eventually bring all of this data together in a paper on the flora of the Santa Monica Mountains at the beginning of the 20th century.

This annotated checklist is a waypoint toward completing a flora of the lichens and lichenicolous fungi of the Santa Monica Mountains at the beginning of the 21st century, which will establish a

Figure 1. Herman Hasse in Civil War uniform,
probably at an annual Veteran's celebration at
Old Soldier's Home near Santa Monica where
he was a doctor.

new historical baseline. This is a work in progress (Knudsen and Lendermer 2007a) and should
not be considered definitive.

It should be kept in perspective that unlike vascular plants, individual lichens generally have
widespread distribution patterns though they may be rare throughout their total range. Many
species are probably millions of years older than plant species. The current distribution of lichens
in southern California, Europe, and North America partially represents the disruption of a
widespread temperate flora by the major glacial events of the last ice age (Knudsen 2005b). Many
rare species in southern California are probably Pleistocene relicts. Others may be new species
that evolved during the post-Pleistocene development of California's Mediterranean climate
(Knudsen & Lendemer 2007a). Nonetheless, cismontane southern California is "new" land that
emerged along the edge of the Pacific Plate relatively recently in a geologic time frame. Lichen
spores often are less than 15 microns long and less than ten microns wide and propagules often do
not exceed a diameter of 50-150 microns. Viability is unknown, but they are small enough to be
dispersed by wind. Several species with unusual distributions not easily explained in the
framework of plate tectonics and climatic history may have arrived here on the winds when fresh
substrate was first exposed or even in relatively recent times.

The lichen flora of both California and North America is so poorly known that the raw
distributional data for biogeography is severely limited. This can be said of every area on earth
except major parts of Europe. But even in Europe new taxa and records continue to be reported.

The taxonomy and systematics of lichens are developing rapidly. As many as twenty species new
to science that occur in southern California will be published in 2007. Currently 1,575 lichen taxa
are reported from California (Tucker and Ryan 2006).

METHODS

The following checklist covers collections by the author since 2003 from the east end of the range in Griffith Park in the city of Los Angeles to the west end in Ventura County. A small amount of collections by others were also used in preparing this checklist. Surveys were conducted on federal, state, and city properties as well as on private property. Part of this work was funded by co-operative agreements between the National Park Service and the University of California at Riverside.

Specimen identifications were determined using current lichen literature, especially the three volumes of the Lichen Flora of the Greater Sonoran Region (Nash et al 2002, 2004, 2007), authentic and type specimens, and the opinion of various experts. James C. Lendemer supplied thin layer chromatography analysis of some specimens and J.A. Elix supplied high performance liquid chromatography and thin layer chromatography analysis of *Lepraria* specimens. Most determinations were re-verified during the writing of the checklist. Several genera are covered scarcely or not at all though they are important components of the flora, including *Aspicilia* and *Arthonia*, as these genera are currently under revision by other authors of the Sonoran Lichen Flora Project and final treatments were not available at time of writing. Several species reported in "Lichens of the Santa Monica Mountains, Part One" (Knudsen 2005a) are currently excluded because of revisionary work as the study of the flora continues. In this checklist we begin the discussion of species only collected by Hasse before 1915. A continuation of this floristic study is intended to be published in 2008 in Vol. 5 of *Opuscula Philolichenum.*

All collections, unless otherwise noted, are by the author (usually with co-collectors) and only the number is cited. Only a representative number of collections are listed with brief location data. All collections by the author are deposited in the Herbarium at the University of California at Riverside. More detailed information is available online at the UCR Herbarium website http://sanders5.ucr.edu/lichensflat_index.php. Duplicates have been distributed to a number of important herbaria, including H, NY, MIN and PH.

Next to each species name is listed its growth form (crustose, foliose, fruticose, squamulose). An explanation of these forms can be found in most books on lichens. They are as accurate as using herb, shrub or tree for classification. Next is listed its substrate preference: saxicolous (rock-loving), corticolous (bark-loving), lichenicolous (parasitic or parasymbiont on lichens), lignicolous (wood-loving), or terricolous (soil-loving). Lichenicolous species may be either lichens (though sometimes with an initial phase of being non-lichenized) or fungi that are not lichenized.

Abbreviations used are: C (calcium hypochlorite), Co (county), NPS (National Park Service), P (potassium hydroxide), SMM (Santa Monica Mountains), SMMRA (Santa Monica Mountains Recreational Area), SP (state park). For definitions of other lichen terminology used in the annotated checklist as well as for more information on individual species, see *Lichen Flora of the Greater Sonoran Region* (Nash et al 2002, 2004, 2007) which also covers southern California. Observations of rarity or abundance are subjective and relative to this phase in the floristic study.

RESULTS: ANNOTATED CHECKLIST OF THE LICHENS AND LICHENICOLOUS FUNGI OF THE SANTA MONICA MOUNTAINS

Acarospora badiofusca (Nyl.) Th.Fr.   Crustose: Saxicolous.

A. badiofusca is common in southern California and the SMM. LA Co: Leo Carrillo SP, ridge between Nicolas and Willow Canyon #4352; Ventura Co: Mishe Mokwa Trail, SMMRA #5648.

Acarospora bullata Anzi   Crustose: Saxicolous.

A. bullata is rare in the SMM but specimens are beautiful dark reddish brown and non-effigurate. It is common inland in California from Riverside to Inyo County where it is usually effigurate, yellowish-brown or blackish-brown, and is found on desert slopes. LA Co: Hepatic Gulch, off Schueren Road #661.

Acarospora dispersa H. Magn.   Crustose: Saxicolous.

This is a member of the *smaragdula* group, with usually one apothecium per areole. It is common in the southeastern United States, but so far known from only a few locations in California, where it was first collected by Robertsons on Mount Diablo. Originally this species was reported as *smaragdula* var. *smaragdula* (Knudsen 2005a). LA Co: Latigo Canyon #1584.

Acarospora elevata H. Magn.   Crustose: Saxicolous.

A. elevata is best developed at higher elevations in the mountains where it occurs in California and Colorado and is a shiny deep brown. At lower elevations in cismontane southern California it is reduced and dull and is often found on small rocks and pebbles. The shiny character depends on the thickness of the syncortex (Knudsen 2007). Its type locality is in the San Gabriel Mountains, a Hasse collection (FH!). LA Co: Leo Carrillo SP, ridge between Nicolas and Willow Canyon #4353.

Acarospora fuscata (Schrad.) Arnold   Crustose: Saxicolous.

This areolate crust is a brown temperate species common in Canada and eastern North America as well as Europe. It is uncommon in the SMM, occurring on sandstone outcrops. LA Co: Calabasas Peak Motorway #700.

Acarospora obnubila H. Magn.   Crustose: Saxicolous.

This brown *Acarospora* is polymorphous but distinguished by its well-developed stipe and algal layer usually interrupted by hyphal bands, except possibly when the algal partner is over-stimulated by nitrates. It is a non-obligate parasite on *Aspicilia* species, but becomes independent of its host. LA Co: Royce Canyon, Griffith Park #5814, #5920; Ventura Co: Mishe Mokwa Trail, SMMRA #814, #5670.

Acarospora obpallens (Nyl. *ex* Hasse) Zahlbr.   Crustose: Saxicolous, Terricolous. **Plate 1.**

A. obpallens is abundant in the SMM on sandstone and can occur on soil. The type locality of *A. obpallens* was near the Old Soldier's Home (now the Veteran's Hospital) on Wilshire Blvd. LA Co: Calabasas Peak Motorway #701; Ventura Co: near Pacific View Road, above Deer Creek Canyon #5624.

Acarospora oligospora (Nyl.) Arnold   Crustose: Saxicolous.

This brown *Acarospora* forms small verrucae and usually occurs on small rocks and pebbles. Large spores, fifty or sixty per ascus, distinguish it from every other species of *Acarospora* in southern California except *A. theloccocoides*, which occurs only on soil. It is infrequent. LA Co: Royce Canyon, Griffith Park #2345; Ventura Co: near Pacific View Road, above Deer Creek Canyon #5597.

Acarospora oreophila K. Knudsen   Crustose: Saxicolous.

This is a brown montane species with a type locality in the San Jacinto Mountains (Knudsen 2007). Los Angeles County: Castro Crest # 1572.

Acarospora robiniae K. Knudsen   Crustose: Saxicolous. **Plate 2.**

This newly described species of yellow *Acarospora* (Knudsen 2007) occurs on Santa Cruz Island and along the coast from Santa Barbara County to Baja Sur in Mexico. It is restricted in the SMM to the western end of its range as are several maritime species. Its cortex is C+ red. Ventura Co: north slope of Conejo Mountain #4059.1.

Acarospora scabrida Hedl. ex H. Magn.   Crustose: Saxicolous.

This bullate brown *Acarospora* occurs in the northwest end of the range with a form matching specimens from Finland. It is rare in California (Knudsen 2005b). Ventura Co: Point Mugu SP: below cliffs above high tide level #4067.2.

Acarospora schleicheri (Ach.) A. Massal.   Crustose: Terricolous.

I have been unable to find this species in the SMM or Verdugo Mountains. Hasse reported it from both ranges at "lower elevations" (Hasse 1913). These areas are now mostly developed. It needs thin-soiled habitat that is undisturbed, especially by invasive weeds and grasses. LA County: Santa Monica range, various Hasse collections (NY! FH!).

Acarospora smaragdula var. *lesdainii* (Harm. *ex* A.L. Smith) H. Magn.   Crustose: Saxicolous.

This is another probable Pleistocene relic and is rare in North America though common from northern Europe to Russia. *Acarospora hassei* Herre is a synonym which was applied to a population in the Santa Cruz Mountains of central California. LA Co: Castro Crest #707.

Acarospora socialis H. Magn.   Crustose: Saxicolous.

This is the common species of yellow *Acarospora* in the SMM and occurs throughout the range on sandstone and volcanic rock. Its type locality is the mountains of Santa Catalina Island. Hasse variously referred to this polymorphic species as *A. xanthophana* and *A. chlorophana*, both names now applied to other taxa. (Hasse 1913) LA Co: Agoura Hills, ridge above Cornell Corners #589.

Acarospora terricola H. Magn.   Crustose or Squamulose: Terricolous.

This is a rare species of western North America that occurs on soil. The type is a Hasse collection from SMM (W!). This is the first record of this species from the SMM since its original collection. Ventura Co: S. of Pacific View Drive between Deer Creek road and Yerba Buena Canyon #5608.

Acarospora thelococcoides (Nyl.) Zahlbr.   Crustose: Terricolous.

This species occurs strictly in thin-soiled openings in coastal sage scrub and chaparral from Baja to central California at Pinnacles National Monument in San Benito County. It is a regional endemic. Its type locality was the mesas of San Diego County where Orcutt first collected it. Thin-soiled habitats supporting biological crusts in southern California contain many rare lichen species and liverworts. They are on the decline and have been heavily impacted by invasive vascular weeds (Knudsen & Magney 2006). This species was probably once common in SMM but it is now rare. LA Co: Agoura. *Tarja Sagar*, n.s. (hb. Sagar); Ventura County: Long Grade Canyon, base of range. *Riefner* #03-209 (UCR).

Acarospora veronensis A. Massal.   Crustose: Saxicolous.

This brown *Acarospora* is common in the SMM. It is a small crust, often pioneering new surfaces and small stones, and is easily overlooked. *Acarospora cinereoalba* (Fink) H. Magn. was reported from the SMM (Knudsen 2005a) but is now considered a synonym of *A. veronensis* (Knudsen 2007). LA Co: Agoura Hills, ridge above Cornell Corners #600.2, #608; Rocky Oaks Park #678.1.

Aspicilia glaucopsina (Nyl. *ex.* Hasse) Hue   Crustose: Terricolous, rarely Saxicolous.

This dull gray crust is so far recorded only from southern California and is rare (Knudsen & Magney 2006). It literally coats spike moss and mosses and lacks any secondary metabolites. Its type locality is the now unknown location of Barton's Peak in the SMM (Hasse 1913). The main population appears to be in the Sandstone Peak area where scattered specimens have been collected. It also occurs in Topanga Canyon and inland from Castro's Crest. The major populations occur in Weir Canyon in the Santa Ana Mountains in Orange County and

on the western slope of the San Jacinto Mountains in Riverside County. Ventura Co: S. of Pacific View Drive between deer Creek road and Yerba Buena Canyon, #5586.

Buellia alboatra (Hoffm.) Th. Fr.   Crustose: Saxicolous (in southern California).

This common white crust with submuriform spores is infrequent in southern California except on the Channel Islands. Ventura Co: NW slope along Yerba Buena Rd #3700.

Buellia badia (Fr.) A. Massal.   Crustose: Lichenicolous, Saxicolous.

B. badia is common in the SMM. It is lichenicolous, growing on a number of hosts including *Acarospora obpallens* and *Aspicilia* species. It becomes independent, forming chocolate-brown squamulose crusts with black lecideine apothecia on sandstone and volcanic rock. Sometimes only its apothecia are apparent on host. LA Co: Griffith Park, Royce Canyon #2348; Ventura Co: north side of Conejo Mountain #4022.

Buellia disciformis (Fr.) Mudd   Crustose: Corticolous.

B. disciformis is rare in the SMM on *Ceanothus cuneatus*. It is distinguished from the common *B. punctata* by its white thallus and larger spores with pointed ends. LA Co: Wugan property (NPS) #3966.

Buellia dispersa A. Massal.   Crustose: Saxicolous.

B. dispersa is infrequent in the SMM. Ventura Co: Mishe Mokwa Trail (SMMRA) #5246.

Buellia pullata Tuck.   Crustose: Saxicolous.

This thin brown areolate crust occurs along the coast and in cismontane canyons in California. LA Co: Malibu, Zuma Canyon #6265; Ventura Co: Point Mugu SP, Chumash Trail #3990.

Buellia punctata (Hoffm.) A. Massal.   Crustose: Corticolous.

This common crust occurs throughout the SMM on the bark and wood of many shrubs and trees. LA Co: Griffith Park, Mount Hollywood #2370; Ventura Co: Sandstone Peak #1963.2.

Buellia ryanii Bungartz   Crustose: Saxicolous.

B. ryanii was named from collections from Santa Cruz Island. It occurs at higher elevations near the coast in the SMM and is distinguished by its spidery prothallus and lecideine apothecia. Its epihymenium turns a pale violet in nitric acid. A similar looking taxon that is undescribed contains norstictic acid. LA Co: Latigo Canyon #1580; Ventura Co: Sycamore Canyon #3686.

Buellia sequax (Nyl.) Zahlbr.   Crustose: Saxicolous, Terricolous.

B. sequax is common throughout California and the SMM. A poorly developed thallus, which is often dull white, distinguishes *B. sequax* from *B. pullata* as does the hard-to-find conidia. A very similar terricolous species is undescribed. LA Co: Griffith Park, Mount Hollywood #2362; Ventura Co: Sycamore Canyon #3708.

Buellia stellulata (Taylor) Mudd   Crustose: Saxicolous

B. stellulata is a common coastal species of the northern hemisphere but is infrequent in the SMM. LA Co: off Kanan Dume Road #623.2.

Buellia tesserata Körb.   Crustose: Saxicolous.

B. tesserata has a distinctive prothallus and is a common maritime species usually found growing in southern California with *Dimelaena radiata*. Ventura Co: north slope of Conejo Mountain #4016.

Buelliella inops (Triebel & Rambold) Hafellner   Lichenicolous fungus.

B. inops grows on *Caloplaca* species. This specimen occurred on *Caloplaca bolacina*, a new host (Hafellner 2004). Verified by Javier Etayo. Ventura Co: Point Mugu SP: below cliffs above high tide level #4062.

Caloplaca albovariegata (de Lesd.) Wetmore   Crustose: Saxicolous.

This gray subsquamulose crust is locally common on Conejo volcanics in the Saddle Peak area. Its epihymenium is K+ violet. Ventura Co: Party Rock above Carlisle Valley #4091.

Caloplaca arenaria (Pers.) Müll. Arg.   Crustose: Saxicolous.
    C. arenaria is a common North American species with small dark reddish-orange apothecia and an endolithic thallus. LA Co: Zuma Ridge #623.2.
Caloplaca atroflava (Turner) Mong.   Crustose: Saxicolous.
    C. atroflava has a gray thallus and is rare in the SMM on volcanic rock. LA Co: stream bed off of Little Sycamore Canyon Road #4091.
Caloplaca bolacina (Tuck.) Herre   Crustose: Saxicolous.
    C. bolacina is common along the California coast and in southern California occurs inland in Riverside County. The thallus is bright orange, subsquamulose and distinctive. LA Co: Off Kanan Dume Road #628. Ventura Co: S. of Pacific View Drive between Deer Creek Road and Yerba Buena #5619.
Caloplaca citrina (Hoffm.) Th. Fr.   Crustose: Saxicolous, Corticolous.
    C. citrina is a common orange leprose crust on shaded rock. LA Co: Royal Oaks Park #677.
Caloplaca crenulatella (Nyl.) Oliv.   Crustose: Saxicolous.
    C. crenulatella is endolithic and commonly found in drainages. LA Co: Henessey (NPS land) #4319.
Caloplaca demissa (Körb.) Arup & Grube   Crustose: Saxicolous.
    C. demissa is a brown sterile crust made up of small elongated lobes. It is infrequent on Conejo volcanics and can be found at scattered sites across southern California. Ventura Co: Conejo Mountain # 4004 (UCR).
Caloplaca epithallina Lynge   Lichenicolous fungus.
    C. epithallina is common in the SMM and parasitic usually on saxicolous *Aspicilia* species. It turns its host thallus into a gray mass. LA CO: Mandeville Canyon # 5277; Zuma Ridge #802; Ventura Co: SMMRA, Mishe Mokwa Trail #5680.
Caloplaca holocarpa (Hoffm. *ex* Ach.) M. Wade   Crustose: Corticolous.
    C. holocarpa is the most common species of *Caloplaca* on the bark of chaparral and coastal sage shrubs. LA Co: Mandeville Canyon #5277; Royal Oaks Park #977.
Caloplaca ignea Arup   Crustose: Saxicolous.
    C. ignea is effigurate with convex lobes. Its bright red color is distinctive and impressive on a sunny day. Locally common on volcanic rock outcrops. Ventura Co: Party Rock above Carlisle Valley #4004.
Caloplaca impolita Arup   Crustose: Saxicolous.
    C. impolita is an effigurate species with light orange lobes with yellow pruina occurring along the coast of California. Ventura Co: Point Mugu SP: base of cliffs above high tide level # 4064.1.
Caloplaca ludificans Arup   Crustose: Saxicolous.
    The type locality of *C. ludificans* is the cliffs of Point Dume (see Figure 2). It's a maritime species and usually occurs with a yellowish-white crustose thallus. When the thallus is lacking, it can be confused with *C. luteominia,* which differs in having thicker, raised apothecial margins. LA Co: Backbone Trail, W of Saddle Peak #4364; Ventura Co: Leo Carrillo SP, Arroyo Sequit, #3715.
Caloplaca luteominia var. **bolanderi** (Tuck.) Arup   Crustose: Saxicolous.
    C. luteominia var. *bolanderi* has a reddish disc. It has less ecological amplitude than var. *luteominia,* appearing to be restricted directly to the coast. The southwestern aspect of the coast of the SMM seems too arid for it and it grows in shaded riparian areas near the beach. Determination verified by Clifford Wetmore. Ventura Co: Leo Carillo SP, Arroyo Sequit, #3723.
Caloplaca luteominia (Tuck.) Zahlbr. var. **luteominia**   Crustose: Saxicolous, Terricolous.
    Var. *luteominia* is common in SMM on rock and soil and is easily identified by its thick, raised non-thalline apothecial margin. LA Co: Kanan Dume Road #5130; Ventura Co: Sycamore Canyon #3706.

Caloplaca nashii Nav.-Ros., Gay & Hladun   Crustose: Saxicolous.

    C. nashii is similar to *C. crenulatella* (which has larger spores); it is endolithic and occurs in drainages. Ventura Co: Point Mugu SP: Chumash Trail #4011.

Caloplaca stellata Wetmore & Kärnfelt   Crustose: Saxicolous.

    C. stellata is an effigurate orange crust with soralia on the lobe tips, occurring locally in the SMM in the Deer Creek area. Ventura Co: Deer Creek #4071.

Caloplaca subsoluta (Nyl.) Zahlbr.   Crustose: Saxicolous.

    C. subsoluta is a common crust that is apparently infrequent in the SMM. LA Co: Leo Carrillo SP, Arroyo Sequit #3719.

Candelaria pacifica Wahlb. *In prep.*   Crustose: Corticolous, Saxicolous.

    C. pacifica is the common species occurring on bark in the SMM. *C. concolor*, which is similar but has over 30 spores per ascus instead of eight spores, is expected. LA Co: Griffith Park, Mount Hollywood #2365; Wagun property (NPS) #3967.

Candelariella aurella (Hoffm.) Zahlbr.   Crustose: Saxicolous.

    C. aurella has bright yellow apothecia and is common on sandstone in the SMM. LA Co: Castro Crest #1575.

Candelariella citrina de Lesd.   Crustose: Saxicolous.

    C. citrina is infrequent on Conejo volcanics. LA Co: Wugan property (NPS) #5171; Ventura Co: S. of Pacific View Drive between Deer Creek road and Yerba Buena Canyon #5608.

Candelariella rosulans (Müll. Arg.) Zahlbr.   Crustose: Saxicolous.

    C. rosulans forms bright yellow subsquamulose rosettes and was collected on Conejo volcanics. Ventura Co: Party Rock above Carlisle Valley #4006.

Catapyrenium squamellum (Nyl. *ex* Hasse) J.W. Thomson   Squamulose: Terricolous.

    C. squamellum is currently a globally rare species known from only eight collection sites worldwide in California, Arizona and Jamaica in over a hundred years (Knudsen 2006). Its description was based on two Hasse collections from SMM (Hasse 1898). He collected no more specimens and ultimately did not include it in his flora (Hasse 1913). The species may be extirpated from the SMM. The nomenclature is revised for reasons discussed in Knudsen and Lendemer 2006. LA Co: Santa Monica Range, Hasse (FH).

Chrysothrix candelaris (L.) J.R. Laundon   Crustose: Corticolous, Saxicolous.

    C. candelaris, a bright yellow leprose crust, usually occurs on *Quercus agrifolia* and on rocks under the oaks in the shade. Ventura Co: Leo Carillo SP, Arroyo #3745.

Cladonia chlorophaea (Flörke ex Sommerf.) Spreng.   Squamulose: Terricolous.

    C. chlorophaea is the most common species in the SMM, occurring in small populations. LA Co: Hepatic Gulch, off Schueren Road #646.1; Castro Crest #711.

Cladonia fimbriata (L.) Fr.   Squamulose: Lignicolous.

    C. fimbriata grows on rotting wood and is more common at higher elevations in the mountains. This specimen was collected by Betsey Landis from a stump of *Ceanothus cuneatus* in an old-growth *Juglans californica* grove. LA Co: W side of Mandeville Canyon *Betsy Landis* s.n. (UCR).

Cladonia hammeri Ahti   Squamulose: Terricolous.

    C. hammeri is endemic to southern California and Baja. It is rare in the SMM. The collection cited below is a rather poor specimen. A single Hasse collection from SMM was determined as *C. hammeri* by Ahti as a paratype in original description (Ahti & Hammer 2002). LA Co: Agoura #607.2.

Cladonia nashii Ahti   Squamulose: Terricolous.

    C. nashii occurs in scattered locations throughout the SMM. It was described by Ahti from Santa Rosa Island (Ahti & Hammer 2002). It is described in the protologue as having farinose soredia on the podetia. Although specimens that are old are very granular, the "granules" are really consoredia which are conglomerations of ecorticate soredia laced together by narrow adventitious hyphae (in this species) and appear to be produced above the cortex; they are not

soralia. The species is often very white near the coast but can be quite brown in hot inland locations like ridges. It contains atranorin and fumarprotocetraric acid. LA Co: Mandeville Canyon #5269; Ventura Co: north slope of Conejo Mountain #4028.

Cladonia pulvinella S. Hammer   Squamulose: Terricolous.

C. pulvinella is a rare species known from only a few sites in California and Baja, including a single location in the SMM. LA Co: Topanga Canyon #351.

Cladonia pyxidata (L.) Hoffm.   Squamulose: Terricolous.

C. pyxidata is locally common in the SMM on Castro Crest, often occurring with *C. chlorophaea*. LA Co: Castro Crest #713, #719.

Cladonia subfimbriata Ahti   Squamulose: Terricolous, Lignicolous.

C. subfimbriata is infrequent in the SMM. It prefers shady areas in mature woodland and chaparral. LA Co: Zuma Ridge #809; Santa Monica Range, Hasse, Lichens Exsiccati #57, collected July, 1914 (UCR), det. by K. Knudsen.

Collema coccophorum Tuck.   Squamulose: Terricolous.

C. coccophorum appears to be less common than *C. tenax* in the SMM. It is most easily distinguished by its two-celled spores. LA Co: along road to Nicholas Flats # 3944.

Collema crispum (Huds.) F. H. Wigg.   Foliose: Terricolous.

C. crispum is apparently infrequent in the SMM. LA Co: Mandeville Canyon #5279.

Collema furfuraceum (Arn.) Du Rietz   Foliose: Corticolous, Saxicolous.

C. furfuraceum is infrequent in the SMM. It was collected off a moist shaded rock. LA Co: Side canyon off Kanan-Dume Rd #4083.

Collema tenax (Sw.) Ach.   Foliose: Terricolous.

This common terricolous cyanolichen has spores that are four-celled or submuriform. It is common in the SMM. Ventura Co: Leo Carillo SP, Arroyo Sequit #3728.

Cyphelium brunneum W.A. Weber   Crustose: Saxicolous.

C. brunneum is only known in the SMM from the north side of the Conejo Mountains (Knudsen and Magney 2006) and is a rare maritime species (Tibell and Ryan 2004). Ventura Co: Conejo Mountain #4029 (UCR).

Dermatocarpon americanum Vain.   Squamulose: Saxicolous.

The gray *D. americanum* is common throughout the SMM on drainages. Ventura Co: Party Rock above Carlisle Valley #4002.

Dimelaena radiata (Tuck.) Müll. Arg.   Crustose: Saxicolous.

D. radiata is the most common maritime lichen in the SMM on rock. Ventura Co: P. Mugu SP, base of cliffs above high tide level, common #4069 (UCR); north slope of Conejo Mountain #4043.

Diploicia canescens (Dicks.) A. Massal.   Crustose: Corticolous, Saxicolous.

D. canescens is common along the coast and on the Channel Islands. It is usually on bark, but can form some impressive specimens on rock. It is infrequent in the SMM. LA Co: Mandeville Canyon *Betsy Landis* s.n. (UCR); Santa Monica Range, Hasse Lichens Exsiccati No. 223, collected May, 1908 and determined as *Pyxine sorediata* (Ach.) Mont. (UCR); Ventura Co: north slope of Conejo Mountain #4048.

Diploschistella athalloides (Nyl.) Lücking, K. Knudsen & Fryday   Crustose: Terricolous.

Diploschistella athalloides is called *Rhizocarpon athalloides* in Hasse's lichen flora (1913) and no doubt specimens of it were determined for Hasse by Nylander. It was common at the beginning of the 20th century in foothills of the SMM that are now mostly developed in the Santa Monica-Brentwood area. For a modern description see Lücking, Knudsen & Fryday 2007. This is one of a number of terricolous lichens Hasse collected in this area of "grassy hills" near the Old Soldier's Home (Hasse 1913) and may have been extirpated from southern California. It is not extinct and still occurs in southern and central Europe. It may still be rediscovered. LA Co: Santa Monica Range, Hasse's Lichenes Exsiccati No. 246 (FH!); Santa Monica Mountains Hasse #788 (FH!).

Diploschistes actinostomus (Ach.) Zahlbr.   Crustose: Saxicolous.

D. actinostomus is rare in the SMM. Ventura Co: north slope of Conejo Mountain #4039.

Diploschistes diacapsis (Ach.) Lumbsch   Crustose: Terricolous.

D. diacapsis forms thin, non-lichenicolous thalli over soil and is rare in the SMM. LA Co: Hepatic Gulch, near Schueren Road #650.

Diploschistes muscorum (Scop.) R. Sant.   Crustose: Lichenicolous, Terricolous, Saxicolous.

D. muscorum is a juvenile parasite on *Cladonia* species. Its thallus surface is always pruinose. On sandstone it must be carefully distinguished from *D. scruposus* which is usually epruinose. LA Co: Agoura #607.

Diploschistes scruposus (Schreb.) Norman   Crustose: Saxicolous.

D. scruposus is common on sandstone in the SMM. LA Co: Topanga State Park #3760.

Endocarpon loscosii Müll. Arg.   Squamulose: Terricolous.

E. loscosii has a scattered distribution pattern in California and is infrequent in the SMM.Ventura Co: Leo Cabrillo State Park, Arroyo Sequit #3737.

Endocarpon pallidulum (Nyl.) Nyl.   Squamulose: Saxicolous.

E. pallidulum occurs on rock in riparian canyons on the coastal side of the SMM. LA Co: Leo Cabrillo SP, Arroyo Sequit #3718.

Endocarpon pseudosubnitescens Breuss   Squamulose: Saxicolous.

This was only the third collection of *E. pseudosubnitescens* and the first in California. The other two locations are in Baja CA, Mexico. The SMM population was destroyed in 2006 when a canyon was backfilled to build a road. LA Co: Off Kanan Road #617.

Endocarpon pusillum Hedwig   Squamulose: Terricolous.

E. pusillum is the most common species of this genus in southern California and is common though often sparse in the SMM. LA Co: Agoura Hills #609.

Evernia prunastri (L.) Ach.   Foliose: Corticolous.

E. prunastri is rare in the SMM and appears to be associated with old-growth chamise chaparral. Increased fire frequency has made old-growth chaparral rare (Knudsen 2006). LA Co: Wugan property (NPS) #3792.

Flavoparmelia caperata (L.) Hale   Foliose: Corticolous, Saxicolous.

F. caperata is a pollution-sensitive foliose lichen that is rare in the SMM probably more from increased fire frequency than air pollution. LA Co: W side of Mandeville Canyon #4080.

Flavopunctelia flaventior (Stirton) Hale   Corticolous, Saxicolous.

F. flaventior is a large foliose lichen found on branches of *Quercus agrifolia*. It is the most common lichen on oaks in the SMM. LA Co: Leo Carrillo SP, Nicholas Flat #3925.

Flavopunctelia soredica (Nyl.) Hale   Foliose: Corticolous, Saxicolous.

F. soredica is infrequent in the SMM and usually occurs on rocks. LA Co: Leo Carrillo SP, Nicholas Flat #3926.2.

Fuscopannaria californica (Tuck.) P.M. Jørg.   Squamulose: Saxicolous.

F. californica is infrequent, occurring in the Saddle Rock area and riparian areas, easily overlooked on volcanic outcrops. Ventura Co: south of Pacific View Drive, top of Deer Creek Canyon #5593.

Hypogymnia imshaugii Krog   Foliose: Corticolous.

H. imshaugii is rare in the SMM in old-growth chamise chaparral. LA Co: Wugan property (NPS) #3977.

Hypogymnia mollis Pike & Hale   Foliose: Corticolous.

H. mollis is rare in the SMM (Knudsen 2005c). LA Co: ridge east of Willow Canyon, Leo Carrillo SP #4357

Kaernefeltia merrillii (DuRietz) Thell & Goward   Foliose: Corticolous.

K. merrillii is another foliose lichen associated with old-growth chaparral that is rare in SMM probably because of increased fire frequency. LA Co: Wugan property (NPS) #3976.

Lecania brunonis (Tuck.) Herre   Crustose, Squamulose: Saxicolous.

L. brunonis is the most common *Lecania* in the SMM. It occurs on sandstone. LA Co: Castro Crest, on sandstone outcrops #1980.1.

Lecania cyrtella (Ach.) Th. Fr.   Crustose: Corticolous.

L. cyrtella is common on the bark of chaparral and coastal sage shrubs. LA Co: Carrillo State Park #4358.

Lecania franciscana (Tuck.) K. Knudsen & Lendemer   Crustose: Saxicolous.

L. franciscana is a maritime crust that is rare in the SMM but common on the Channel Islands (Knudsen and Lendemer 2007b). Santa Monica range, Hasse (UCR).

Lecania fructigena Zahlbr.   Crustose: Saxicolous.

L. fructigena is maritime in distribution and is common on the west coast from central California to Baja and on the Channel Islands, but rare in the SMM. Ventura Co: P. Mugu SP: Chumash Trail # 3983.2 & #4110.

Lecania hassei (Zahlbr.) W. Noble   Squamulose: Saxicolous.

L. hassei is rare on shaded sandstone and has its type locality in Topanga Canyon (Knudsen and Lendemer 2007b). Malibu Creek # 7143.1.

Lecania toninioides Zahlbr.   Crustose: Saxicolous, Terricolous.

L. toninioides is rare in the SMM but is common from its type locality, the Ballona Bluffs, south to Baja California. It is known in the literature as a terricolous lichen but is quite common in southern California on sandstone and decaying granite and occurs as far inland as Riverside at an elevation of 384 meters on the campus of UCR on clay. LA Co: off Little Sycamore Canyon Road # 5166.1.

Lecanora caesiorubella Ach.   Crustose: Corticolous.

L. caesiorubella is common on *Quercus agrifolia* especially in canyons along the coast. LA Co: Leo Carrillo SP, Nicholas Flats #4344.

Lecanora circumborealis Brodo & Vitik.   Crustose: Corticolous.

L. circumborealis was collected on poison oak vines in a coastal canyon, but is more common on *Quercus agrifolia.* LA Co: Side canyon off Kanan-Dume Rd # 4085.

Lecanora gangaleoides Nyl.   Crustose: Saxicolous.

L. gangaleoides is easily recognized because of its black apothecia and white thallus and is only similar to *Tephromela* species. Ventura Co: South of Pacific View drive between Deer Creek Road and Yerba Buena Canyon #5628.

Lecanora hagenii (Ach.) Ach.   Crustose: Corticolous, Lignicolous, Saxicolous.

This endolithic crust is common in coastal canyons of the SMM on volcanic rock. LA Co: Malibu Canyon #7133.

Lecanora laxa (Iiwa & Wetmore) Printzen   Crustose: Corticolous.

L. laxa is easily overlooked on the bark of shrubs. It is usually collected above 1000 m. LA Co: Wugan property (NPS) #3968.2.

Lecanora muralis (Schreb.) Rabenh.   Crustose: Saxicolous.

L. muralis is the most common saxicolous *Lecanora* in southern California, naturally occurring as a component of various lichen communities. It usually only becomes dominant when factors such as air pollution eliminate its competition. Ventura Co: Leo Carrillo SP, Arroyo Sequit #3733.

Lecanora pacifica Tuck.   Crustose: Corticolous.

L. pacifica is common on oak bark in the SMM. LA Co: Leo Carrillo SP, Nicholas Flats #4336.

Lecanora polytropa (Hoffm.) Rabenh.   Crustose: Saxicolous.

L. polytropa is common at higher elevations in the southern California mountains, esp. above 1500 m. A specimen was collected on a single sandstone outcrop in the SMM. Such montane species were probably more common during the ice age. LA Co: Henessey (NPS land), #4316.

Lecanora pseudistera Nyl.   Crustose: Saxicolous.

L. pseudistera is the most common member of the *Lecanora subfusca* group on rock in southern California. Some specimens in the SMM resemble *Trapeliopsis glaucopholis* but *L. pseudistera* is K+ yellow and C-. LA Co: Topanga State Park #3921.

Lecanora subimmergens Vain.   Crustose: Saxicolous. **Plate 3.**

L. subimmergens is common on sandstone in the SMM and Santa Ana Mountains. It is reported new to California (Tucker & Ryan 2006). Determined by James C. Lendemer. Ventura Co: Leo Carrillo SP, Arroyo Sequit #3743.

Lecanora strobilina (Sprengel) Kieffer   Crustose: Corticolous, Lignicolous.

L. strobilina occurs along the coast in southern California at scattered locations. Ventura Co: P. Mugu SP: Chumash Trail 3997.1.

Lecidea austrocalifornica Zahlbr.   Crustose: Saxicolous, Terricolous.

L. autrocalifornia Zahlbr. is currently under re-evaluation and may prove to be a synonym of a *Lecidella* (Christian Printzen, pers. comm..) It was treated as a Mycobilimia in Knudsen 2005a, and is currently under study. LA Co: Near Old Soldier's Home. Hasse, Lectotype (H!)

Lecidea cinerata Zahlbr.   Crustose: Saxicolous.

The type locality of *L. cinerata* was on "decaying granite in the Santa Monica Range above Hollywood" (Hasse 1913). Granite is rare in the SMM with large exposures in this general area, but most of the area has been developed for housing. *L. cinerata* may be extirpated from the SMM, but no extensive surveying has been done in its type locality. It is endemic to the southern California area and is probably a high elevation species preferring shaded humid locations on hard granite (Knudsen & Kramer 2007). LA Co: Santa Monica Range. H.E. Hasse #1195 (FH!).

Lecidea confluens (Web.) Ach.   Crustose: Saxicolous.

L. confluens occurs in the SMM on sandstone. Most specimens are ashy gray. Like *L. diducens* Nyl., western specimens so far have a non-amyloid reaction to iodine though European specimens are regularly amyloid. It has also been collected on Santiago volcanics in the Santa Ana Mountains (Knudsen 1545, UCR). It is reported as new to California (Tucker & Ryan 2006). It was probably determined by Hasse as *Lecidea plana* but so far we have seen neither specimens of *L. plana* nor the related *L. lithophila* from southern California. Based on poor TLC data, this species was first reported as *L. plana* (Knudsen 2005a). Specimens contained confluentic acid and 2-O-methylperlatolic acid. LA Co: Zuma Ridge # 803.

Lecidea fuscoatra (L.) Ach.   Crustose: Saxicolous.

This species has a brown or gray thallus and C+ red cortex. It is common on sandstone and is well adapted to vertical road cuts. LA Co: Malibu Creek State Park, along Backbone Trail, S of Stunt Road #7129.

Lecidea laboriosa Müll. Arg.   Crustose: Saxicolous.

L. laboriosa is usually endolithic with polymorphic apothecia. It is the most common *Lecidea* in southern California. It generally occurs on sandstone in the SMM and often develops a thallus. LA Co: Topanga SP #3921.

Lecidea mannii Tuck.   Crustose: Saxicolous.

L. mannii is infrequent on sandstone and has a C+ red cortex. It occurs in Baja CA, Mexico and southern California as well as Chile and Patagonia. LA Co: Castro Crest #1573.

Lecidea truckeei Herre   Crustose: Saxicolous.

L. truckeei is rare in the SMM and was collected on sandstone. It is a generally high elevation species occurring from Baja CA, Mexico to Oregon above 2000 meters. *L. schizopeltica* Hertel & Leuckert is a synonym (Lendemer & Knudsen 2007). LA Co: Malibu SP, along Backbone Trail #7119.2.

Lecidella asema (Nyl.) Knoph & Hertel   Crustose: Corticolous, Lignicolous, Saxicolous, Terricolous.

L. asema is common on rock in maritime communities of southern California. *Lecidea catalinaria* Stizenb. is a synonym. Hasse often determined this and other saxicolous *Lecidella* species as either *Lecidea subplebeia* or *Lecidea enteroleuca*. Ventura Co: North slope of Conejo Mountain # 4340.

Lecidella carpathica Körb.   Crustose: Saxicolous.

L. carpathica is common in southern California and occurs on sandstone in the SMM. LA Co: Topanga SP #3758.

Lecidella stigmatea (Ach.) Hertel & Leuckert   Crustose: Saxicolous.

L. stigmatea is common in southern California and was collected on volcanic rock in the SMM. LA Co: Mishe Mokwa Trail #5666.

Lempholemma chalazanum (Ach.) de Lesd.   Crustose: Terricolous.

L. chalazanum was once common on soil in the foothills of the SMM. It is rare in California. The first collection in the SMM in almost a hundred years was made in 2005 (Knudsen 2005c). LA Co: Leo Carrillo SP, Willow Canyon #4363; foothills near Soldiers' Home, Hasse # 892 (FH!).

Lepraria adheraens K. Knudsen, Elix & Lendemer   Crustose: Saxicolous, Terricolous. **Plate 5.**

L. adheraens is common in cismontane southern California from the SMM to coastal San Diego. It also occurs in Pennsylvania and the Ozarks. It has a blue hue, contains pannarin and zeorin and is P+orange. This is one of three newly described *Lepraria* species that are common in the SMM (Knudsen, Elix & Lendemer 2007). LA Co: Latigo Canyon: #1586.

Lepraria santamonicae K. Knudsen & Elix   Crustose: Saxicolous, Terricolous.

L. santamonicae is a new species discovered in Griffith Park and so far is known only from the Santa Monica and Santa Ana Mountains. It contains argopsin and norargopsin (Knudsen & Elix 2007a). LA Co: Griffith Park #4380 (holotype).

Lepraria texta K. Knudsen, Elix & Lendemer   Crustose: Saxicolous. **Plate 6.**

L. texta is a new species discovered on Conejo volcanics in the Sandstone Peak area. Currently it is considered endemic to southern California. It contains atranorin (major or minor), usnic acid (major), zeorin (minor), roccellic and/or angardianic acid (minor) (Knudsen & Elix 2007b). Ventura Co: Party Rock #5153 (holotype); LA Co: Malibu Creek #7142.

Leprocaulon microscopicum (Vill.) Gams *ex* D. Hawksw.   Crustose, Squamulose: Terricolous.

L. microscopicum is common in maritime communities in southern California but is rare in the SMM. Ventura Co: North slope of Conejo Mountain #4020.

Leptogium tenuissimum (Dicks.) Körb.   Foliose: Terricolous.

This small cyanolichen is often overlooked. It is apparently infrequent in the SMM but often found near the coast in California. Ventura County: NPS property above Little Sycamore Canyon Road #7154.

Letharia vulpina (L.) Hue   Foliose: Corticolous.

L. vulpina is rare in the SMM. Bryologist Tarja Sagar's collection is from old-growth *Adenostoma fasciculatum*. LA Co: Backbone Trail north of Camp 15 at Encinal Canyon Road. *Tarja Sagar,* s.n.; Santa Monica Range, Hasse exsiccate #64, collected April, 1910 (UCR).

Lichinella cribellifera (Nyl.) P. Morena & Egea   Foliose: Saxicolous.

L. cribellifera is a foliose cyanolichen that is larger than *L. nigritella* and lacks isidia. One population was found. Ventura Co: SMMRA: Mishe Mokwa Trail #5645.

Lichinella nigritella (Lettau) P. Moreno & Egea   Foliose: Saxicolous.

L. nigritella has isidia and is smaller than *L. cribellifera*. It is known currently from a single population in the SMM. LA Co: off Little Sycamore Canyon Road #5160.

Melanohalea elegantula (Zahlbr.) O. Blanco *et al.*   Foliose: Corticolous, Saxicolous.

M. elegantula is commonly found on granite and sandstone in the SMM though generally it is more common on bark throughout its range. Acidification of bark by nitrates may be a factor

in the poverty of foliose lichens in the SMM as well as *M. elegantula's* occurrence on rock. Synonym: *Melanelia elegantula* (Zahlbr.) Essl. LA Co: Hepatic Gulch, near Schueren Road, #655.1.

Micarea denigrata (Fr.) Hedl.   Crustose: Corticolous, Saxicolous.

M. denigrata is usually collected on bark but was found on rock. Determined by Alan Fryday. LA Co: Topanga State Park #3913.2.

Micarea deminuta Coppins   Crustose: Lignicolous.

M. deminuta occurs usually on damp wood and has simple spores. It was determined by Brian Coppins from a Hasse collection recently and is reported as a new record for North America in Vol. 3 of the Lichen Flora of the Greater Sonoran Region (Fryday & Coppins 2007). Hasse #771 LA Co: Santa Monica Range (NY).

Micarea erratica (Körb.) Hertel, Rambold & Pietschm.   Crustose: Saxicolous.

M. erratica is known from a single Hasse collection in the SMM recently determined by Alan Fryday (Fryday & Coppins 2007). This is an apparently rare species in California, though common in eastern North America and Europe. It is a small crust occurring on rocks and pebbles with biatorine apothecia, hyaline spores without septation, and an areolate gray crust. This is one of many species collected by Hasse but not found in recent times. Hasse #958 Santa Monica Range (NY).

Miriquidica mexicana Rambold, Sipman & Hertel   Crustose, Squamulose: Saxicolous.

M. mexicana is infrequent in the SMM. The relation of this species to *Miriquidica scotopholis* (Tuck.) B.D. Ryan & Timdal needs taxonomic clarification and it is probably a synonym (Knudsen and Owe-Larsson 2005). Ventura Co: Sandstone Peak # 2488.

Mobergia angelica (Stizenb. *ex* Hasse) H. Mayrhofer & Sheard   Crustose: Saxicolous, Terricolous.

M. angelica is common in the SMM. It is endemic to the southwestern coast of North America from central California to Baja Sur and Guadalupe Island. LA Co: Zuma Ridge # 804; Kanan Dune Rd #999.

Muellerella lichenicola (Sommerf. & Fr.) D. Hawksw.   Lichenicolous fungus.

M. lichenicola is a lichenicolous fungus occurring on a large number of hosts. This specimen occurred on *Lecanora pseudistera*. Ventura Co: Leo Carrillo SP, Arroyo Sequit # 3734.2.

Niebla cephalota (Ach.) Rundel & Bowler   Fruticose: Corticolous.

N. cephalota is abundant north of the SMM and on the Channel Islands but infrequent in the SMM. LA Co: Leo Carrillo SP, Nicholas Flats #4351.

Niebla ceruchoides Rundel & Bowler   Fruticose: Saxicolous.

N. ceruchoides and the following *Niebla* species are all members of maritime communities and occur only on the north side of Conejo Mountain in the SMM. Ventura Co: North slope of Conejo Mountain # 3951 (UCR).

Niebla homalea (Ach.) Rundel & Bowler   Fruticose: Saxicolous.

Ventura Co: North slope of Conejo Mountain #4055.

Ochrolechia subpallescens Vers.   Crustose: Corticolous.

O. subpallescens occurs on bark of *Quercus agrifolia*. LA Co: Royal Oaks #679.

Parmotrema chinense (Osbeck) Hale & Ahti   Foliose: Corticolous.

Parmoterma chinense occurs on the bark of *Quercus agrifolia*. It is infrequent in the SMM, which is the southern limit of its range in California. LA Co: Leo Carrillo SP, Nicholas Flats #4336.

Peltula bolanderi (Tuck.) Wetmore   Squamulose: Saxicolous.

P. bolanderi is a cyanolichen and is similar to *P. euploca*. Both species are found in drainages and are common in the SMM. LA Co: Agoura Hills #604.

Peltula euploca (Ach.) Poelt   Squamulose: Saxicolous.

P. euploca is apparently less common than *P. bolanderi* in the SMM. Ventura Co: north side of Conejo Mountain #4055.

Peltula obscurans var. **hassei** (Zahlbr.) Wetmore   Squamulose: Saxicolous, Terricolous.

P. obscurans var. *hassei* is infrequent in the SMM. Hasse first discovered the species in the San Jacinto Mountains near Palm Springs and did not report it from the SMM (Hasse 1913). LA Co: Hornwort Gulch, off of Cold Canyon Road #705.

Peltula patellata (Bagl.) Swinscow & Krog   Squamulose: Terricolous.

P. patellata, which Hasse knew as *Heppia polyspora* Tuck., is infrequent in small populations in the SMM on sandstone or soil over volcanic rock. LA Co: Agoura # 588.

Pertusaria amara (Ach.) Nyl.   Crustose: Corticolous.

P. amara is common on the bark of *Quercus agrifolia.* LA Co: Leo Carrillo State Park: Nicholas Flat #3935.

Pertusaria flavicunda Tuck.   Crustose: Saxicolous.

The yellowish *P. flavicunda* is so far known only from the Nicolas Flats area. LA Co: Leo Carrillo SP #4348.

Pertusaria velata (Turner) Nyl.   Crustose: Corticolous, Saxicolous.

P. velata occurs on the bark of *Quercus agrifolia.* Dibbins considered the SMM populations a separate species, *P. santamonicae.* The SMM specimens are rich in xanthones. LA Co: Leo Carrillo SP, Nicholas Flats #4343.

Phaeophyscia hirsuta (Mereschk.) Essl.   Foliose: Corticolous, Saxicolous.

P. hirsuta is a common species and can be found on bark or rock. It is usually much reduced and mixed with other lichens, thus easily overlooked. LA Co: Point Mugu SP: #4064.2.

Physcia adscendens (Fr.) H. Olivier   Foliose: Corticolous, Saxicolous.

P. adscendens is common on the bark of coastal sage and chaparral shrubs throughout the SMM. Ventura Co: Top of Deer Creek # 4072.2.

Physcia dimidiata (Arnold) Nyl.   Foliose: Saxicolous.

P. dimidiata looks very similar to *P. tribacia.* It is more common than *P. tribacia* and there is no clear delimitation between their distributions in the SMM. LA Co: Side canyon off Kanan-Dume Rd #4082.

Physcia tribacia (Ach.) Nyl.   Foliose: Saxicolous.

P. tribacia is less common in the SMM than *P. dimidiata.* LA Co: off Schueren Road # 647.

Physconia fallax Essl.   Foliose: Corticolous, Saxicolous.

P. fallax is more common on rock than bark in the SMM. LA Co: Party Rock above Carlisle Valley #4094.

Physconia isidiigera (Zahlbr. *ex* Herre) Essl.   Foliose: Corticolous, Saxicolous.

P. isidiigera is more common on rock than on bark in the SMM. LA Co: Hepatic Gulch, near Schueren Road #655.2.

Placidium lacinulatum (Ach.) Breuss   Squamulose: Terricolous.

P. lacinulatum is frequent in the SMM. Ventura Co: Sandstone Peak #2482.

Placidium squamulosum (Ach.) Breuss   Squamulose: Terricolous.

P. squamulosum is a common terricolous lichen infrequently found throughout the SMM. LA Co: along Kanan Dume Road #999; Hornwort Gulch along Cold Canyon Road #1973.1.

Placynthiella icmalea (Ach.) Coppins & P. James   Crustose: Terricolous.

P. icmalea is only known in the SMM at this time from sandstone outcrops on Castro Crest. It has a C+ red thallus. LA Co: Castro Crest #1577.1.

Placynthiella knudsenii Lendemer   Crustose: Terricolous.

P. knudsenii is known in the SMM from three collections in the Saddle Peak area. It is rare throughout southern California and is often associated with detritus at base of chamise chaparral. These three specimens may prove to be a new species distinguished by smaller spores on an average and a red subhymenium (Christian Printzen, pers. comm.) LA Co: Below Sandstone Peak #1964.

Placynthiella uliginosa (Schrad.) Coppins & P. James   Crustose: Terricolous.
P. *uliginosa* is apparently rare in the SMM, often growing among mosses and *Cladonia* populations. It is infrequent throughout southern California but is under-collected. LA Co: Off Schueren Road #646.2.

Polysporina lapponica (Ach. *ex* Schaer.) Degel.   Crustose: Saxicolous, Lichenicolous.
P. *lapponica* is common on sandstone in the SMM, especially in the Topanga Canyon area. It has wider spores and larger apothecia than *P. simplex*. Its most common host is *Acarospora obpallens*. *Sarcogyne bicolor* H. Magn., with a type locality on Point Dume, is a synonym. LA Co: Topanga Canyon #1552.

Polysporina simplex (Davies) V zda   Crustose: Saxicolous, Terricolous.
P. *simplex* is common in the SMM, especially on the higher elevation sandstone outcrops where sometimes it is the only lichen in an area. LA Co: Calabasas Peak Motorway #702.

Psora decipiens (Hedwig) Hoffm.   Squamulose: Saxicolous, Terricolous.
P. *decipiens* is infrequent in the SMM and currently known only from a few locations. It is more common inland especially on carbonate-derived soils. LA Co: Hepatic Gulch, near Schueren Road #663.2.

Psora luridella (Tuck.) Fink   Squamulose: Saxicolous, Terricolous.
P. *luridella* was once common on grassy hills that are in the Brentwood-Santa Monica area (Hasse 1913) and is common inland. It is rare on ridges in the SMM. It is C-. The K test can be deceptive, looking somewhat reddish, but it contains no secondary metabolites. Usually to test dubious spot reactions, also wet lichen with water and see if you get same color hue when thallus is hydrated. LA Co: ridge between Sullivan and Mandeville Canyon #5283.

Psora pacifica Timdal   Squamulose: Terricolous.
P. *pacifica* is infrequent in the SMM and in southern California, occurring below 400 meters in hills near the coast. Often populations are small and easily overlooked. C+/KC+ red cortex. LA Co: Agoura Hills #587.

Psora russellii (Tuck.) A. Schneider   Squamulose: Saxicolous, Terricolous.
P. *russellii* is known only from pillow basalt along Cold Canyon Road in the SMM. It is more common in the desert. LA Co: Hornwort Gulch, off of Cold Canyon Road #669.

Punctelia perreticulata (Räsänen) G. Wilh. & Ladd   Foliose: Corticolous, Saxicolous.
P. *perreticulata* is a large gray foliose lichen that grows on the bark of *Quercus agrifolia* and on volcanic rock in the SMM; it is infrequent. LA Co: Leo Carrillo SP: Nicholas Flat #3926.1.

Punctelia punctilla (Hale) Krog   Foliose: Saxicolous.
Rick Riefner, Jr. collected *P. punctilla* from the Conejo Mountain area and so far no new populations have been verified. It has also been collected from Baja Sur. The SMM collection appears to be a relict of a past flora, possibly an ancient tropical flora. The species is common in South America and South Africa (Egan & Aptroot 2004, Knudsen and Magney 2006). Ventura Co: western end of range. Riefner #20-249 (UCR).

Pyrrhospora quernea (Dicks.) Körb.   Crustose: Corticolous.
P. *quernea* is generally associated with maritime lichen communities on bark. It is infrequent near the coast on coastal sage and chaparral shrubs. Ventura Co: n/s of Conejo Mountain #4049.1.

Ramalina farinacea (L.) Ach.   Fruticose: Corticolous.
Hasse said *R. farinacea* was common throughout southern California (1913); it is the most common *Ramalina* found today in southern California. LA Co: Leo Carrillo SP, Nicolas Flat # 3928 & #3939.2.

Ramalina leptocarpha Tuck.   Fruticose: Corticolous.
R. *leptocarpha* is endemic to central and southern California near the coast. It is infrequent in the SMM. LA Co: Leo Carrillo SP, Nicholas Flats #4341.

Ramalina menziesii Taylor   Fruticose: Corticolous.

R. menziesii was once common in southern California to 800 meters (Hasse 1913). Development and air pollution has no doubt helped make it rare in southern California. Development through paving and buildings has caused a decrease in ground fog, which was once frequent and dense in the valleys and grasslands of southern California and is an important source of moisture for lichens. This probably also contributed to its disappearance from more arid inland locations in oak woodlands. LA Co: Santa Monica Range, Hasse Exsiccati No. 22 (UCR); Leo Carrillo SP, Silke Werth SM007A (UCR); Ventura Co: Point Mugu SP: Chumash Trail #3995.

Ramalina pollinaria (Westr.) Ach.   Fruticose: Corticolous.

R. pollinaria was once frequent on shrubs in the SMM (Hasse 1913) but it is now rare. LA Co: Leo Carrillo SP, Nicholas Flats#4349.

Ramonia ablephora (Nyl *ex* Hasse) R.C. Harris   Crustose: Terricolous.

R. ablephora is known from only a single collection by Hasse (1898) but was not included in his flora (1913). R.C. Harris lumped it with *Ramonia gylectiformis* (Zahlbr.)V zda and they are treated as a single species in Vol. 2 of the Sonoran lichen flora (Ryan and Nimis 2004). Knudsen and Lendemer, consulting with R.C. Harris and with fresh specimens collected of *R. gylactiformis* from San Jacinto Mountains, found the two species distinct (Knudsen and Lendemer 2005), a change recognized in Vol. 3 of the Sonoran flora (Knudsen & Lendemer 2007a). *Ramonia ablephora* is a terricolous lichen and may be extinct in the wild. It is probably endemic to the SMM. LA Co: Santa Monica Mountains, Hasse (Isotype, NY).

Rinodina endospora Sheard   Crustose: Corticolous.

R. endospora is endemic to California and was collected on *Juglans californica* in a woodland that had not burned in 75 years. Its range in the SMM needs further study. This collection had blastidia, was determined by Sheard, and for the time being is probably best considered *endospora s. lato*. LA Co: Mandeville Canyon #5272.

Rinodina gennarii Bagl.   Crustose: Saxicolous.

R. gennarii is frequent in the SMM near the coast especially in riparian areas of canyons. LA Co: Latigo Canyon #1581; Leo Carrillo SP, Arroyo Sequit #3724.2.

Rinodina intermedia Bagl.   Crustose: Terricolous.

R. intermedia is a terricolous lichen with pseudomuriform spores that is common in southern California from the coast inland to the base of the mountains. It is infrequent in the SMM. LA Co: Agoura Hills #599.

Rinodina parasitica H. Mayrh. & Poelt   Crustose: Saxicolous, Lichenicolous.

R. parasitica is frequent in the western portion of the SMM in coastal canyons. It is parasitic on *Aspicilia* species and other crustose lichens. LA Co: road to Nicholas Flats #3924; Ventura Co: North slope of Conejo Mountain #5143.

Sarcogyne arenosa (Herre) K. Knudsen and Standley   Crustose: Saxicolous.

S. arenosa is infrequent on sandstone in the SMM. LA Co: Topanga Canyon #1564.

Sarcogyne privigna (Ach.) A. Massal.   Crustose: Saxicolous.

S. privigna is distinguished from *S. reebiae* by joint lines in the margin of the apothecia (Knudsen & Standley 2007). It generally occurs in drainages, even on rocks of riverbeds. It is under-collected, and frequent in the SMM. Ventura Co: South of Pacific View Drive, top of Deer Creek Canyon #5623.

Sarcogyne reebiae K. Knudsen   Crustose: Saxicolous. **Plate 4.**

S. reebiae is similar to *S. privigna* in the ontogeny of the apothecium but it forms a smooth round margin without joint lines. It is a newly described species currently only known from southern California. (Knudsen & Standley 2007). LA Co: Topanga SP #3913.2.

Sarcogyne similis H. Magn.   Crustose: Saxicolous.

S. similis is the most common species of this genus in the SMM and is often found on sandstone Outcrops. LA Co: Castro Crest #978; Zuma Ridge #799; Topanga Canyon #1564 & 1567.

Staurothele monicae (Zahlbr.) Wetmore   Crustose: Saxicolous.

S. monicae is found in drainages and is common in the Saddle Peak area. Specimens of *Verrucaria intercedens aethioboloides* Nyl., collected by Hasse (#222, NY!) are this species (a type has not been seen of *V. intercedens aethioboloides* and may differ from specimens examined). Ventura Co: NPS land on hilltop, e/o Little Sycamore Canyon Road #6255.

Strangospora deplanata (Almq.) Clauz. & Roux   Crustose: Corticolous.

S. deplanata is a rare corticolous crust that occurs in mixed chaparral communities on bark in the SMM. Its exciple and epihymenial pigment distinguishes it easily from *S. moriformis*, the most widespread member of this genus in southern California, which has not been found in the SMM so far. LA Co: Wugan property (NPS) #3968.3.

Texosporium sancti-jacobi (Tuck.) Nàdv.   Crustose: Terricolous.

T. sancti-jacobi is a rare lichen that was collected on a ridge above Cornell's Corner. It has legal status because it is listed on the Department of Fish and Game's Special Plants, Bryophytes, and Lichens list (Knudsen and Magney 2006). LA Co: Agoura #598.

Teloschistes chrysophthalmus (L.) Th. Fr.   Fruticose: Corticolous.

T. chrysophthalmus is a beautiful orange lichen that can infrequently be found on chaparral and coastal sage shrubs. LA Co: Leo Carrillo SP, Nicholas Flat #3939.1; Ventura Co: Point Mugu SP: Chumash Trail #4001.

Teloschistes flavicans (Sw.) Norman   Fruticose: Corticolous.

T. flavicans is rare in the SMM but is often found together with *T. chrysophthalmus*. LA Co: Wugan property #5173.

Tephromela nashii Kalb.   Crustose: Saxicolous.

T. nashii is a maritime species. Ventura Co: Conejo Mountain #4021.

Thelocarpon intermediellum Nyl.   Crustose: Saprobic, Fungus (rarely lichenized).

T. intermediellum is a rare species of fungus that is occasionally lichenized. It has yellow pruina. It is saprobic and has been collected on cow dung as well as more collectable pieces of old wood and leather. The single collection from the SMM was made off of a dying *Lecanora muralis* and is a poor specimen mixed with another fungus. No more could be located at the collection site. It appears to be evanescent. Ventura Co: Party Rock above Carlisle Valley #4003.2.

Thelomma mammosum (Hepp *ex* Hartung) A. Massal.   Crustose: Saxicolous.

T. mammosum is common along the coast of western North America and can occur as far as 20 miles from the coast in southern California. Its thallus is KC+ rose-red. LA Co: Kanan Dume Road #5129.

Thelomma santessonii Tibell   Crustose: Saxicolous.

T. santessonii is restricted to the immediate coast and is endemic from Baja to southern California. LA Co: Leo Carrillo SP #3927; off Schueren Road #649; Ventura Co: north side of Conejo Mountain #4036.

Toninia aromatica (Sm.) A. Massal.   Crustose: Lichenicolous, Saxicolous, Terricolous.

T. aromatica is infrequent in the SMM. It can occur as a lichenicole or growing independently. Ventura Co: Point Mugu SP: Chumash Trail. #3983.1.

Toninia subdispersa (**Nyl. *ex* Hasse**) K. Knudsen   Lichenicolous fungus.

T. subdispersa is lichenicolous on *Lecania* species, occurring as small black apothecia usually on thallus of host. (Knudsen and Lendemer 2007b). LA Co: Griffith Park: Royce Canyon #2349.

Toninia submexicana de Lesd.   Crustose: Saxicolous.

T. submexicana is infrequent in the SMM. LA Co: off Little Sycamore Canyon Road #5164.

Trapelia coarctata (Turner ex Sm.) M. Choisy   Crustose: Saxicolous, Terricolous.

T. coarctata is infrequent in the SMM and southern California, occurring usually on north slopes. LA Co: Henessey (NPS land) #432.

Trapelia glebulosa (Sm.) J.R. Laundon   Crustose: Saxicolous, Terricolous.

T. glebulosa is quite variable in thallus forms. It is common throughout the SMM as a pioneer on soil exposed by road cuts and landslides. This species is listed in most books under its incorrect name *Trapelia involuta*. LA Co: Zuma Ridge #798; Ventura Co: Sycamore Canyon #3694.

Trapeliopsis bisorediata McCune & Camacho   Crustose: Terricolous, Saxicolous.

T. bisorediata is infrequent in southern California. Generally occurring on soil, it does grow on small pebbles and has been collected on granite in a drainage and on sandstone. Ventura Co: south of Pacific View Drive, top of Deer Creek Canyon #5611.

Trapeliopsis flexuosa (Fr.) Coppins & P. James   Crustose: Lignicolous.

T. flexuosa is common on decorticated and burnt wood in the SMM and elsewhere in southern California. It should be carefully distinguished from *T. granulosa* (Printzen & McCune 2004). LA Co: Mandeville Caynon #5274; Zuma Ridge #808.

Trapeliopsis glaucopholis (Nyl. *ex* Hasse) Printzen & McCune   Squamulose: Saxicolous, Terricolous.

T. glaucopholis is common in southern California, but is apparently infrequent or poorly developed in the SMM. Some specimens are vaguely similar to specimens of *Lecanora pseudistera*, but differ in the K- & KC+ red reaction of the thallus. *T. californica* is a synonym of T. *glaucopohlis*. LA Co: Zuma Ridge #807.

Trapeliopsis granulosa (Hoffm.)Lumbsch   Crustose: Lignicolous.

T. granulosa is rare at lower elevations but more common above 2000 meters in the mountains. C. Printzen annotated a Hasse collection from SMM as *T. granulosa* and the same exsiccate at UCR is *T. granulosa*. As with all Hasse exsiccati it should not be assumed that all specimens with same number are *T. granulosa*. Hasse only recognized *T. flexuosa* as occurring in the SMM (1913). *T. granulosa* appears to occur in the eastern part of the range. The thalli of both species intergrade and when infertile can be hard to determine. LA Co: Lichenes Exsiccati Hasse #196 (ASU & UCR); Griffith Park: Bronson Canyon #2374.

Usnea glabrata (Ach.) Vain.   Fruticose: Corticolous.

U. glabrata usually occurs near the coast. It is rare in the SMM. It is interesting that in his flora Hasse listed no *Usnea* as occurring in the SMM (1913). Two species were collected in one location on old-growth chamise chaparral (Knudsen 2006). LA Co: Wugan property (NPS) #3971.

Usnea flavocardia Räsänen   Fruticose: Corticolous.

U. flavocardia is rare on old-growth chaparral and has red spots on its thallus. It is better known by the synonym of *U. wirthii*. LA Co: Wugan property (NPS) #3938.

Usnea lapponica Vain.   Fruticose: Corticolous.

U. lapponica is infrequent in the Nicholas Flats area on *Malacothamnus*. LA Co: Leo Carrillo SP, Nicholas Flats #4343.

Verrucaria calkinsiana Servit   Crustose: Saxicolous.

V. calkinsiana occurs in drainages on sandstone and small stones. It appears to be fairly frequent in southern California. Determined by Othmar Breuss. Ventura Co: south of Pacific View Drive, top of Deer Creek Canyon, #5611.

Verrucaria cetera Breuss   Crustose: Saxicolous.

V. cetera is a silver-pruinose *Verrucaria* that is parasitic on other lichens usually *Staurothele*. But in this specimen *V. cetera* is parasitic on another *Verrucaria* on a wet drainage on tilted rock slab, a perfect microhabitat for *Staurothele*. LA Co: Griffith Park: Royce Canyon #5815.2.

Verrucaria elaeina Borror   Crustose: Saxicolous.

V. elaeina is a riparian species and was collected in a shaded oak woodland along a perennial stream. Determined by Othmar Breuss. LA Co: Leo Carrillo SP, Arroyo Sequit #3744.

Verrucaria furfuracea (de Lesd.) Breuss   Crustose: Saxicolous.

V. fufufracea is infrequent in the SMM. It is isidiate. It was collected on the grout of an old house foundation. Ventura Co: Conejo Mountain #5150.2.

Verrucaria fusca Pers. *ex* Ach.   Crustose: Saxicolous.

V. fusca becomes gelatinous when the thallus is wetted and has an involucrellum almost completely enclosing the exciple. It occurs in drainages like many *Verrucaria* and *Staurothele*. Ventura Co: west side of Conejo Mountain #5138.

Verrucaria fuscoatroides Servit   Crustose: Saxicolous.

V. fuscoatroides appears to be widespread in southern California. It occurs in the Saddle Peak area on volcanics. It is easily confused with *V. turgida* but *V. fuscoatroides* has an involucrellum contiguous with the exciple. Determined by Othmar Breuss. Ventura Co: SMMRA: Mishe Mokwa Trail #5664 (UCR).

Verrucaria mimicrans Servit   Crustose: Saxicolous.

V. mimicrans was collected in a shaded riparian habitat in SMM. Determined by Othmar Breuss. LA Co: Leo Carrillo SP, Arroyo Sequit #3727.

Verrucaria subdivsa Breuss   Crustose: Saxicolous.

This newly described species is common on the Channel Islands but seems to find the southern aspect of the SMM coastline too hot and is infrequent in coastal canyons. LA Co: Malibu Canyon #7134.

Verrucaria rufofuscella Servit   Crustose: Saxicolous.

V. rufofuscella was collected by Hasse. It is similar to *V. fuscoatroides* and was recently collected with several other infrequent species on shale. Determined by Othmar Breuss. Ventura Co: Point Mugu SP: Chumash Trail #3982.

Verrucaria turgida Servit   Crustose: Saxicolous.

V. turgida belongs to a group of *Verrucaria* with brown thalli. The separation of the involucrellum from the exciple and its large spores distinguish it from other species. LA Co: Malibu Creek State Park, along Backbone Trail, S of Stunt Road, #7126.

Waynea californica Moberg   Crustose: Corticolous.

W. californica occurs on the bark of *Quercus agrifolia* and *Juglans californica* in the SMM and can be easily overlooked. LA Co: Leo Carrillo SP, Nicholas Flat # 4345; W side of Mandeville Canyon, above *Betsy Landis* s.n.

Xanthoparmelia cumberlandia (Gyel.) Hale   Foliose: Saxicolous, Terricolous.

The Henessey and Conejo Mountain populations contain both the common form and a lobulate form of this species on sandstone and volcanic breccia. Coastal populations often occur on soil and may represent a different species (Nash and Elix 2004) LA Co: Henessey (NPS land) #4317; Ventura Co: Sycamore Canyon #3709; north slope of Conejo Mountain #4304.

Xanthoparmelia mexicana (Gyel.) Hale   Foliose: Saxicolous.

X. mexicana is the most common isidiate lichen in southern California and is common throughout the SMM. LA Co: Griffith Park: Royce Canyon #5808; Ventura Co: n/s of Conejo Mountain # 4035.

Xanthoparmelia neotaractica Hale   Foliose: Saxicolous.

X. neotaractica is known from only one location in the SMM, a narrow shaded moist ravine on pillow basalt. LA Co: Hornwort Gulch, off of Cold Canyon Road #1972 (UCR).

Xanthoria elegans (Link) Th. Fr.   Foliose: Saxicolous.

X. elegans is frequent in the SMM. Ventura Co: Party Rock #5142.1

Xanthoria polycarpa (Hoffm.) Rieber   Crustose: Corticolous.

    X. polycarpa is common on chaparral and sagebrush shrubs throughout southern California. LA Co: Small creek near Encinal Canyon Rd #4009.

Xanthoria tenax L. Lindblom   Crustose: Corticolous.

    X. tenax is common on coastal sage scrub and chamise chaparral shrubs in southern California. It is attached by its entire underside directly to bark. It can be mistaken for *X. polycarpa* which is attached by rhizines and has a corticate lower surface. LA Co: Wugan property #3958.

DISCUSSION AND CONCLUSIONS

Despite serious ecological changes including urban development and sprawl, air pollution, grazing, increased fire frequency, invasive weeds, and ornamental landscaping, the Santa Monica Mountains still contain a diverse lichen flora. Two hundred ten lichens and lichenicolous fungi in 74 genera are documented in this annotated checklist. Many more records were not included as they are in the process of determination, verification or revision. More surveys over the whole range as well as the study of herbaria records should increase this number substantially.

New species of lichen being currently described from southern California are known from populations in the Santa Monica Mountains such as *Acarospora robiniae* (type locality Santa Cruz Island), *Lepraria adhaerens* (type locality Torrey Pines State Park), *Lepraria santamonicae* (type locality Griffith Park), *Lepraria texta* (type locality Santa Monica Mountains) and *Sarcogyne reebiae* (type locality Weir Canyon, Santa Ana Mountains).

I have discussed only a few of the lichens known only from Hasse collections. I am sure several of these "missing" species will be re-discovered, but not all them. The clarification of the early 20th century baseline flora and the completion of a 21st century baseline flora will be especially valuable in illuminating this discrepancy between the two historical periods.

Many species collected during the current survey were not collected by Hasse, athough the exact number is not known. It should be noted that Hasse collected more intensively in the eastern half of the Santa Monica Mountains as far west as Malibu. For instance, based on his flora (Hasse 1913), many maritime species which were collected during the current survey on the north slope of Conejo Mountain and the west end of the Santa Monica Mountains in Ventura County are only reported by him from the Channel Islands or farther south in Orange and San Diego County. Another indication of this difference is that more collections by Hasse are on sandstone than on the Conejo volcanics, which predominate in the western part of the range. Another difference is that Hasse did not collect sterile crusts, which are regularly collected during this survey.

From Griffith Park to Point Mugu State Park, a large part of the Santa Monica Mountains is in public trust in city, county, state, and federal parks and preserves. The Santa Monica Mountain Conservancy continues to acquire new land, as does the Santa Monica Mountains National Recreation Area. Nonetheless, some very special areas are still in private property. For instance, the north slope of Conejo Mountain in Ventura County contributed many species of the maritime lichen flora to this checklist that were not collected in the SMM by Hasse. Those slopes support thriving populations of the rare plant species *Dudleya verityi* and *Eriogonum crocatum* too. It is private property but should definitely be preserved. Another unique area is a ridge in Agoura Hills supporting remnants of the old terricolous lichen community on stony, thin soil which includes the only known population of *Texosporium sancti-jacobi* in Los Angeles County. It is private property and should be saved from development. The continued acquisition of selected

pieces of private property is the best way to preserve the unique lichen flora of the Santa Monica Mountains. Those lichens that can still be found in the SMM have survived air pollution, increased fire frequency, and urban sprawl. Their continued survival depends especially on habitat conservation.

A lost opportunity is illustrated by *Endocarpon pseudosubnitescens* Breuss. It is a unique squamulose and saxicolous lichen described by Othmar Breuss from only two collections by Thomas Nash and Bruce Ryan from Baja CA, Mexico. The third location was found on shaded volcanic rock in a mesic side canyon off Kanan Dume Road on private property. It was reported new to North America (as defined as north of Mexico) and California (Knudsen 2005a). It was buried beneath yards of backfill in 2006 to build a road to an isolated parcel where a small number of new houses were being built. Currently no new populations have been discovered.

ACKNOWLEDGEMENTS

Plate 1. *Acarospora obpallens* (Nyl. ex Hasse) Zahlbr.

Plate 2. *Acarospora robiniae* K. Knudsen.

Plate 3. *Lecanora subimmergens* Vain.

Plate 4. *Sarcogyne reebiae* K. Knudsen.

Plate 5. *Lepraria adhaerens* K. Knudsen, Elix & Lendemer.
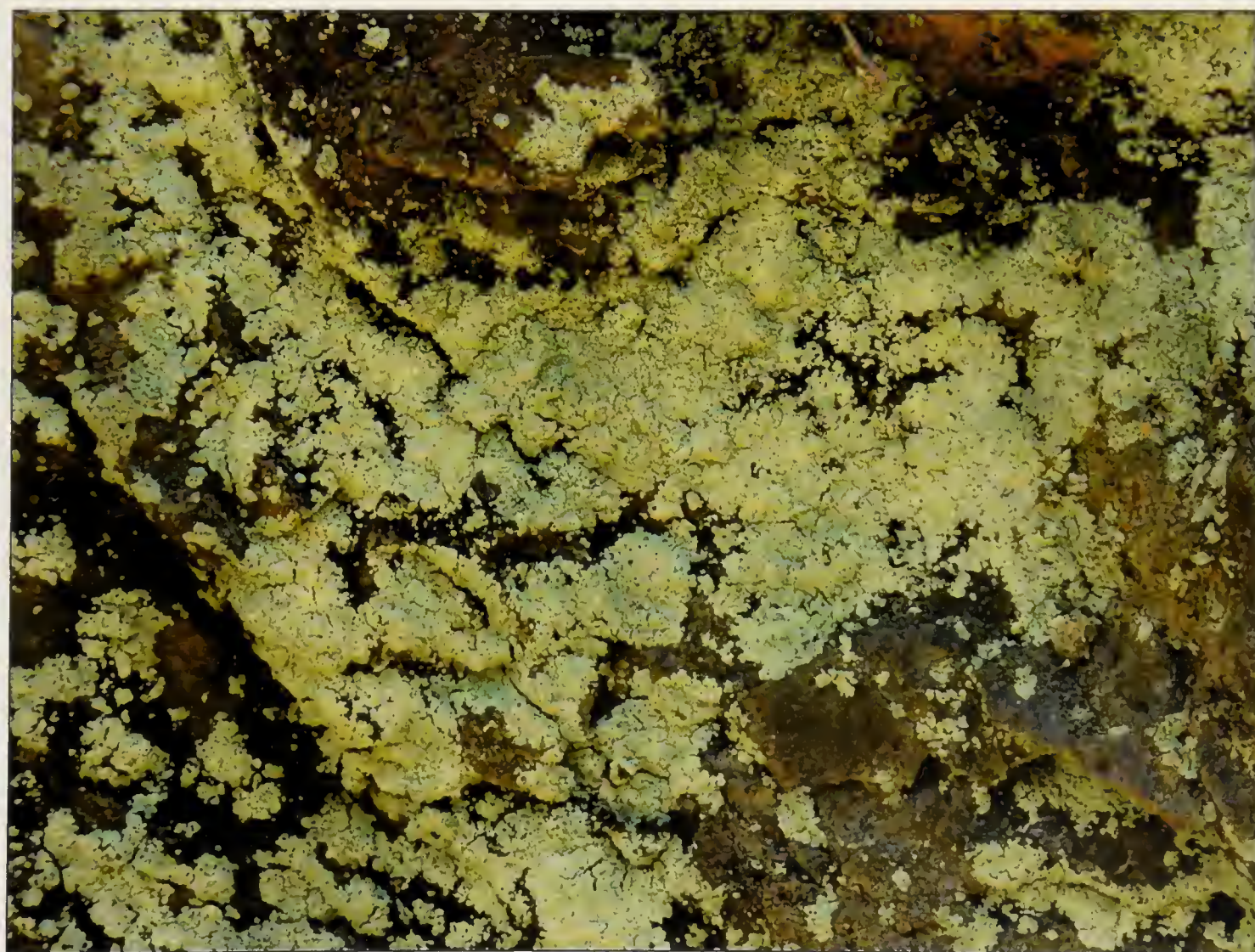
Plate 6. *Lepraria texta* K. Knudsen, Elix & Lendemer.

Plate 7. *Niebla* with *Dudleya veritiyi.*

Plate 8. Maritime lichen community on north slope of Conejo Mountain.

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BRYOPHYTES OF THE SANTA MONICA MOUNTAINS

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With images from Arlee Montalvo, Janet Walle, Carl Wishner, and Carly Ryan

ABSTRACT: A preliminary species list is provided for bryophytes of the Santa Monica Mountains, along with illustrations of representatives of many of the genera to serve as an introductory guide to the group. Presently 109 species of bryophytes are known from the Santa Monica Mountains. This does not count some of the species from difficult genera with many samples of uncertain identification remaining to be studied further. *Bryoerythrophyllum ferruginascens* (Strit.) Giac. is reported new for California. A comparison of the Santa Monica Mountains bryophyte flora with those of Santa Cruz County, at the same elevation but higher latitude, and Mount San Jacinto, at the same latitude but higher elevation, indicates that the Santa Monica Mountains flora shares more of its species with Santa Cruz County but lacks a great many species that are common in that wetter climate, and that the Santa Monica Mountains flora is remarkably dissimilar in composition to the flora of Mount San Jacinto.

KEYWORDS: Bryophytes, California, mosses, Santa Monica Mountains

NARRATIVE ANALYSIS OF THE FLORA

The Santa Monica Mountains, on the southern coast of California within Los Angeles and Ventura counties, fall within the semi-arid mediterranean climate regime where a non-bryologist might not expect to find very many bryophytes. Yet, bryophyte species richness is not particularly inhibited by regional aridity when wet spots exist within the region. The Santa Monica Mountains have a complex geomorphology of ridges and narrow drainages, several of which have perennial or nearly perennial water flow. A few northern species find suitable habitat in the deeper cooler drainages. In addition, a few species from warm, dry places to the west and south also find suitable microhabitats. These two elements contribute to a checklist that is currently at 109 species. Although perhaps surprising to non-bryologists, this number is not extraordinary for a region of such strong relief (Shevock 2003).

The Santa Monica Mountains are home to all three kinds of bryophytes: hornworts, liverworts and mosses. Four out of seven species of hornworts found in California (Doyle and Stotler 2006) have been collected in the Santa Monica Mountains. Two of these, *Anthoceros punctatus* L. and *Phaeoceros carolinianus* (Michx.) Prosk. *s. l.*, are nearly worldwide in their distribution. The other two have a much narrower range. *Anthoceros fusiformis* Austin has a North Pacific distribution and is known from Japan and the Pacific Coast of North America, and *Phaeoceros pearsonii* (M. Howe) Prosk. is known from Washington to California (Doyle and Stotler 2006).

Although not abundant in the Santa Monica Mountains, hornworts are widely scattered along most streams and ditches, generally on disturbed summer-dry soil and at the edges of seepages, usually shaded by shrubs or trees.

Leafy liverworts, a group of 87 species in California (Doyle and Stotler 2006), are represented in the Santa Monica Mountains by only three species. *Porella bolanderi* (Austin) Pearson, occurring in shaded ravines and north-facing slopes, is the only relatively common and abundant local leafy liverwort. Of the 41 thallose liverwort species in California, 13 have been confirmed from the Santa Monica Mountains. Several species, such as *Asterella californica* (Hampe) Underw. and *Cryptomitrium tenerum* (Hook.) Austin ex Underw., occur on moist shaded sloping soil, while the genus *Riccia* is common on sunnier, flatter soil that floods during heavy rains.

Most of the bryophyte species in the Santa Monica Mountains are mosses. Like the rest of California (Norris and Shevock 2004), the Pottiaceae is the most species-rich family in the Santa Monica Mountains, with 32 species in 14 genera. Pottiaceae contains many species tolerant of long droughts, and not surprisingly, several species are among the most common and abundant in the range. Three of the *Didymodon* species, two species of *Syntrichia* and several species of *Tortula*, for example, occur nearly throughout the mountains and are easily noticed along trails and drainages. Two of the species in this family, *Eucladium verticillatum* (Hedwig *in* Bridel) Bruch & W. P. Schimper and *Crumia latifolia* (Kindberg) W. B. Schofield, are much less tolerant of drying and are confined to perennially wet microhabitats.

Brachytheciaceae is another common family of mosses in the Santa Monica Mountains, with 13 species reported from the range. Bryaceae and Orthotrichaceae are likewise represented by several species, while most of the other families are represented by one or two infrequent species, restricted to certain microhabitats, regardless of apparently abundant suitable habitat. For example, *Leptobryum pyriforme* (Hedwig) Wilson, common farther north and a nearly cosmopolitan species that does well on disturbed sites such as creek banks, has been observed in small patches only in three locations in the Santa Monica Mountains. *Encalypta rhaptocarpa* Schwägrichen, the only representative of its family in the Santa Monica Mountains, has been observed only in three locations although there are plenty of similar habitats throughout the range. Other species tolerant of arid conditions that one would expect to find in the Santa Monica Mountains have not yet turned up in the collections. *Encalypta vulgaris* Hedwig, for example, frequently found in the western United States and Mexico and known to be more tolerant of arid conditions than *Encalypta rhaptocarpa* Schwägrichen (Flowers 1973), has not yet been reported from the Santa Monica Mountains. *Bryolawtonia vancouveriensis* (Kindberg) Norris & Enroth and the feathery *Dendroalsia abietina* (W. J. Hooker) E. Britton *in* Brotherus, both endemic to Western North America and abundant along the central and north coast of California, are examples of species for which the Santa Monica Mountains are near the southern extension of their range. They are known here only from a few locations in deep narrow perennial drainages with dense canopies.

It is instructive to compare the bryoflora of the Santa Monica Mountains to two other well-documented bryofloras. Mount San Jacinto (in Riverside County), whose bryophytes were studied by Harpel (1980), is at the same latitude but more inland and mostly at a higher elevation than the Santa Monica Mountains. Santa Cruz County, whose bryophytes were catalogued by Kellman (2003), is coastal and at roughly the same elevation as the Santa Monica Mountains but at higher latitude and thus is much moister and cooler. Santa Cruz County, at 190 species, far outnumbers both the Santa Monica Mountains and Mount San Jacinto, each of which have species lists that are around 100. Furthermore, both Santa Cruz County and Mount San Jacinto have several more genera and families represented in their flora than we have found in the Santa

Monica Mountains. The greater bryophyte diversity of California's central coast is probably due to the temperate moister climate and our better understanding of the Santa Cruz County flora. Kellman's (2003) collections in the 1990's more than doubled the number of county records available for study and significantly increased our understanding of the region.

The Santa Monica Mountains share about a third of their species with Mount San Jacinto and nearly two thirds of their species with Santa Cruz County. Elevation appears to be an important factor in separating bryogeographic zones. Most of the shared species are low to mid-elevation, cosmopolitan or widely distributed species (e.g. *Bryum argenteum* Hedwig, *Didymodon tophaceus* (Bridel) Lisa, *Grimmia pulvinata* (Hedwig) J. E. Smith, *Scleropodium touretii* (Bridel) L. Koch, *Weissia controversa* Hedwig). A few of the species shared by all three areas are endemic to western North America, for example *Scleropodium obtusifolium* (Mitten) Kindberg *in* Macoun, a ropy prostrate moss that forms trailing mats over boulders along streams, and *Anacolia menziesii* (Turner) Paris, a moss that fills the cracks in rocks, easily recognized for its abundant rusty red rhizoids that form a dense tomentum on the lower stems. The other endemic species, such as *Bestia longipes* (Sullivant & Lesquereux) Brotherus (Norris and Enroth 1990, Schofield 2004) and *Dendroalsia abietina* (W. J. Hooker) E. Britton *in* Brotherus (Schofield 1992), occur in both the Santa Monica Mountains and Santa Cruz County, but have not been found in the Mount San Jacinto area which has higher elevations and colder winters.

In a few cases, a species abundant in Santa Cruz County or Mount San Jacinto occurs in the Santa Monica Mountains, but for the most part the suitable habitat is occupied by another species with similar habitat requirements. *Antitrichia californica* Sullivant *in* Lesquereux, known mainly from the west coast of North America (Norris and Shevock 2004), is common along the central coast, but barely makes it into the Santa Monica Mountains and is not abundant in any of its locations here. Instead, the apparent suitable habitat is often occupied by *Pterogonium gracile* (Hedwig) J. E. Smith, a species endemic to west coast of North America from southernmost Canada to southern California (Zander 2006) and shared with Santa Cruz County.

Of the three areas, the Santa Monica Mountains have the fewest species not found in either of the other two. This may be partly an artifact of the majority of the local flora belonging to the difficult genera, such as *Bryum*, *Didymodon*, *Tortula*, and *Trichostomum*, with many samples of uncertain identification remaining to be studied. Presently, the Santa Monica Mountains share nearly twice as many species with Santa Cruz County (65 species) as it shares with Mount San Jacinto (33 species). However, a more thorough survey of seasonal habitats and identification of unresolved collections may reveal the Santa Monica Mountains' bryoflora to be more closely related to the floras of arid lands such as Baja California than to either Santa Cruz County or Mount San Jacinto.

Below we give a list of the bryophytes that we have confirmed identifications for from the Santa Monica Mountains. This is accompanied by a gallery of drawings of representative species of the genera one is most likely to encounter hiking through the range. So far as we can tell at this time, the number of species and the composition of the bryoflora are not unusual for a semiarid west coast region of its size. Nevertheless, we have found species that are major range extensions, specifically, *Didymodon bistratosus* J.-P. Hébrard & R. B. Pierrot formerly only known from Mediterranean Europe (Zander et al. 2005), *Bryoerythrophyllum ferruginascens* (Stirt.) Giac. not previously recorded from California, and *Bryum microchaeton* Hampe a species normally of higher moister regions to the south.

PRELIMINARY CHECKLIST

Nomenclature follows Norris and Shevock (2004) for mosses, and Doyle and Stotler (2006) for liverworts and hornworts. When vouchers have already been deposited in the Herbarium of California State University Northridge (SFV), we cite a specimen following the family name.

Mosses

Aloina ambigua (Bruch & W. P. Schimper) Limpricht [Pottiaceae]

Aloina bifrons (De Notaris) Delgadillo [Pottiaceae] Sagar 1232 (SFV)

Aloina rigida (Hedwig) Limpricht [Pottiaceae]

Amblystegium juratzkanum W. P. Schimper [Amblystegiaceae] McGraw 25 (SFV)

Amblystegium serpens (Hedwig) Bruch & W. P. Schimper [Amblystegiaceae] Sagar 508 (SFV)

Anacolia baueri Hampe [Bartramiaceae] Sagar 423 (SFV)

Anacolia menziesii (Turner) Paris [Bartramiaceae] Sagar 85 (SFV)

Antitrichia californica Sullivant *in* Lesquereux [Leucodontaceae] Sagar 1048 (SFV)

Bestia longipes (Sullivant & Lesquereux) Brotherus [Brachytheciaceae] Sagar 408 (SFV)

Brachythecium albicans (Hedwig) Bruch & W. P. Schimper [Brachytheciaceae] Sagar 244 (SFV)

Brachythecium asperrimum (C. Muller Hal.) Sullivant [Brachytheciaceae] Sagar 81 (SFV)

Brachythecium bolanderi (Lesquereux) A. Jaeger [Brachytheciaceae] Sagar 333 (SFV)

Bryoerythrophyllum columbianum (F. J. Hermann & F. Lawton) Zander [Pottiaceae] Sagar 1087 (SFV)

Bryoerythrophyllum ferruginascens (Stirt.) Giac. [Pottiaceae] Sagar 518 (SFV)

Bryoerythrophyllum recurvirostrum (Hedwig) Chen [Pottiaceae] Sagar 1066 (SFV)

Bryolawtonia vancouveriensis (Kindberg) Norris & Enroth [Neckeraceae] Wishner 2005/09/23.15 (duplicate in SFV)

Bryum microchaeton Hampe [Bryaceae]

Bryum argenteum Hedwig [Bryaceae] Sagar 758 (SFV)

Bryum barnesii Wood *in* W. P. Schimper [Bryaceae] Sagar 384

Bryum capillare Hedwig [Bryaceae] Sagar 950 (SFV)

Bryum comparable to *kunzei* [Bryaceae] Sagar 1041 (SFV)

Bryum lisae [Bryaceae] Sagar 670 (SFV)

Bryum muehlenbeckii [Bryaceae] Sagar 880

Bryum pseudotriquetrum (Hedwig) Gärtner, B. Meyer & Scherbius [Bryaceae] Sagar 1072

Bryum pyriferum Crundwell & H. Whitehouse (=*B. valparaisense*) [Bryaceae] McGraw 18

Ceratodon purpureus (Hedwig) Bridel [Ditrichaceae]

Claopodium whippleanum (Sullivant) Renauld & Cardot [Leskeaceae] Sagar 370 (SFV)

Conardia compacta (C. Muller Hal.) H. Robinson [Campyliaceae] Sagar 377 (SFV)

Crossidium squamiferum (Viviani) Juratzka [Pottiaceae] Sagar 360 (SFV)

Crumia latifolia (Kindberg) W. B. Schofield [Pottiaceae] Sagar 736 (SFV)

Dendroalsia abietina (W. J. Hooker) E. Britton *in* Brotherus [Cryphaeaceae] Sagar 406 (SFV)

Didymodon australasiae (W. J. Hooker & Greville) Zander [Pottiaceae] Sagar 387 (SFV)

Didymodon bistratosus J.-P. Hébrard & R. B. Pierrot [Pottiaceae] Sagar 838 (SFV)

Didymodon brachyphyllus (Sullivant *in* Whipple) Zander [Pottiaceae] Sagar 702 (SFV)

Didymodon nicholsonii Culmann [Pottiaceae] Sagar 30 (SFV)

Didymodon norrisii Zander [Pottiaceae] Sagar 821 (SFV)

Didymodon rigidulus Hedwig [Pottiaceae] Sagar 839 (SFV)

Didymodon tophaceus (Bridel) Lisa [Pottiaceae] Sagar 714 (SFV)

Didymodon vinealis (Bridel) Zander [Pottiaceae] Sagar 117 (SFV)

Ditrichum ambiguum Best [Ditrichaceae] Sagar 369 (SFV)

Encalypta rhaptocarpa Schwägrichen [Encalyptaceae] Wilson 4332 (SFV)

Eucladium verticillatum (Hedwig *in* Bridel) Bruch & W. P. Schimper [Pottiaceae] Sagar 11 (SFV)

Fabronia pusilla Raddi [Fabroniaceae] Wilson 4292 (SFV)

Fissidens bryoides Hedwig [Fissidentaceae] Sagar 347 (SFV)

Fissidens crispus Montagne [Fissidentaceae] McGraw 14 (SFV)

Fissidens sublimbatus Grout [Fissidentaceae] Sagar 576 (SFV)

Funaria hygrometrica Hedwig [Funariaceae] Sagar 751

Funaria muhlenbergii Turner [Funariaceae] Sagar 837

Gemmabryum Species A according to Spence & Ramsy Sagar 831

Grimmia laevigata (Bridel) Bridel [Grimmiaceae] Sagar 575 (SFV)

Grimmia lisae De Notaris [Grimmiaceae] Sagar 425 (SFV)

Grimmia ovalis (Hedwig) Lindberg [Grimmiaceae] Sagar 57 (SFV)

Grimmia pulvinata (Hedwig) J. E. Smith [Grimmiaceae] Sagar 417 (SFV)

Grimmia trichophylla Greville [Grimmiaceae] Sagar 365 (SFV)

Gymnostomum calcareum Nees & Hornschuch [Pottiaceae] Sagar 1040 (SFV)

Hedwigia detonsa (Howe) W. R. Buck & Norris [Hedwigiaceae] Sagar 399 (SFV)

Hennediella stanfordensis (Hedwig) Zander [Pottiaceae] Sagar 1052 (SFV)

Homalothecium aeneum (Mitten) E. Lawton [Brachytheciaceae] Sagar 382 (SFV)

Homalothecium arenarium (Lesquereux) E. Lawton [Brachytheciaceae] Sagar 290 (SFV)

Homalothecium nuttallii (Wilson) A. Jaeger [Brachytheciaceae] Sagar 65 (SFV)

Homalothecium pinnatifidum (Sullivant & Lesquereux) E. Lawton [Brachytheciaceae] Sagar 170 (SFV)

Leptobryum pyriforme (Hedwig) Wilson [Meesiaceae] Sagar 76 (SFV)

Leptodictyum humile (Palisot de Beauvois) [Amblystegiaceae] Sagar 500 (SFV)

Leptodictyum riparium (Hedwig) Warnstorf [Amblystegiaceae] Sagar 484

Microbryum davallianum (J. E. Smith *in* Drake) Zander [Pottiaceae] Wilson 3725 (SFV)

Microbryum starkeanum (Hedwig) Zander [Pottiaceae] Sagar 1097 (SFV)

Orthotricum affine Schader *ex* Bridel [Orthotrichaceae] Sagar 211 (SFV)

Orthotrichum bolanderi Sullivant [Orthotrichaceae] Sagar 372 (SFV)

Orthotrichum flowersii Vitt [Orthotrichaceae] Sagar 241 (SFV)

Orthotrichum hallii Sullivant & Lesquereux in Sullivant [Orthotrichaceae] Sagar 708 (SFV)

Orthotrichum rupestre Schleicher *ex* Schwägrichen [Orthotrichaceae] Sagar 414

Orthotrichum tenellum Bruch *ex* Bridel [Orthotrichaceae] Sagar 504

Phascum cuspidatum Hedwig [Pottiaceae] Sagar 176 (SFV)

Pleuridium subulatum (Hedwig) Rabenhorst [Ditrichaceae] Sagar 1129 (SFV)

Pohlia camptotrachela Renauld & Cardot) Brotherus [Mniaceae] Sagar 1026 (SFV)

Pohlia wahlenbergii (Weber & D. Mohr) Andrews *in* Grout [Mniaceae] Sagar 1110 (SFV)

Pterogonium gracile (Hedwig) J. E. Smith [Leucodontaceae] Sagar 410 (SFV)

Rosulabryum elegans (Nees ex Bridel) Ochyra Sagar 358

Rosulabryum torquescens (De Not.) Spence Sagar 94

Schistidium cinclidodonteum (C. Müller Hal. *in* Röll) B. Bremer [Grimmiaceae] Sagar 206 (SFV)

Scleropodium californicum (Lesquereux) Kindberg [Brachytheciaceae] Sagar 289

Scleropodium cespitans (Wilson *ex* C. Müller Hal.) L. Koch [Brachytheciaceae] Sagar 373 (SFV)

Scleropodium julaceum E. Lawton [Brachytheciaceae] Sagar 456 (SFV)

Scleropodium obtusifolium (Mitten) Kindberg *in* Macoun [Brachytheciaceae] Sagar 261 (SFV)

Scleropodium touretii (Bridel) L. Koch [Brachytheciaceae] Sagar 319 (SFV)

Syntrichia princeps (De Notaris) Mitten [Pottiaceae] Sagar 184 (SFV)

Syntrichia ruralis (Hedwig) Weber & D. Mohr [Pottiaceae] Sagar 398 (SFV)

Timmiella anomala (Bruch *in* W. P. Schimper) Limpricht [Pottiaceae] Wilson 4302 (SFV)

Timmiella crassinervis (Hampe) L. Koch [Pottiaceae] Sagar 49 (SFV)

Tortula atrovirens (J. E. Smith) Lindberg [Pottiaceae] Wilson 4322 (SFV)

Tortula californica E. B. Bartram [Pottiaceae] Sagar 16 (SFV)

Tortula guepinii (Bruch & W. P. Schimper) Brotherus [Pottiaceae] Sagar 1068 (SFV)

Tortula inermis Bridel [Pottiaceae] Sagar 304 (SFV)

Tortula muralis Hedwig [Pottiaceae] Sagar 223

Tortula systylia (W. P. Schimper) Lindberg [Pottiaceae] Sagar 1093

Trichostomum crispulum Bruch *in* F. A. Mueller [Pottiaceae] Sagar 1127 (SFV)

Weissia condensa (Voit in J. W. Sturm) Lindberg [Pottiaceae] McGraw 30 (SFV)

Weissia controversa Hedwig [Pottiaceae] Sagar 505 (SFV)

Liverworts

Asterella bolanderi (Austin) Underw. [Aytoniaceae]

Asterella californica (Hampe) Underw. [Aytoniaceae] Sagar 553 (SFV)

Asterella palmeri (Hampe) Underw. [Aytoniaceae]

Cephaloziella divaricata (Sm.) Schiffn. var. *divaricata* [Cephaloziellaceae] Sagar 259 (SFV)

Cephaloziella turneri (Hook.) Müll. Frib. [Cephaloziellaceae] Sagar 260

Cryptomitrium tenerum (Hook.) Austin *ex* Underw. [Aytoniaceae] Wilson 4273 (SFV)

Fossombronia longiseta (Austin) Austin [Fossombroniaceae] Wilson 3719 (SFV)

Porella bolanderi (Austin) Pearson [Porellaceae] Sagar 449 (SFV)

Porella cordaeana (Huebener) Moore [Porellaceae] Sagar 202

Riccia campbelliana M. Howe [Ricciaceae] Sagar 107 (SFV)

Riccia nigrella DC. [Ricciaceae] Sagar 108 (SFV)

Riccia sorocarpa Bisch. [Ricciaceae] Wilson 3716 (SFV)

Riccia trichocarpa M. Howe [Ricciaceae] Sagar 111 (SFV)

Sphaerocarpos cristatus M. Howe [Sphaerocarpaceae] Sagar 2 (SFV)

Sphaerocarpos texanus Austin [Sphaerocarpaceae] Sagar 870 (SFV)

Targionia hypophylla L. [Targioniaceae] Sagar 103 (SFV)

Hornworts

Anthoceros fusiformis Austin [Anthocerotaceae] Sagar 564 (SFV)

Anthoceros punctatus L. [Anthocerotaceae]

Phaeoceros carolinianus (Michx.) Prosk. [Notothyladaceae] Sagar 552 (SFV)

Phaeoceros pearsonii (M. Howe) Prosk. [Notothyladaceae] Wilson 3730 (SFV)

ACKNOWLEDGEMENTS

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Plate 1: Acrocarpous (upright) mosses

Aloina rigida (Hedwig) Limpricht [Pottiaceae]

Aloina are plants of dry soil barrens that may flood seasonally. They have deeply concave leaves with incurved margins folding over a cushion of photosynthetic filaments. The genus could be confused with *Pterygoneurum* or *Crossidium*, but instead of photosynthetic filaments, *Pterygoneurum* has sheets of cells on the midrib rather than filaments, and lacks the overarching leaf margins present in *Crossidium*. Neither *Pterygoneurum* or *Crossidium* have been found in the Santa Monica Mountains yet. *Aloina bifrons*, also known from the Santa Monica Mountains, has a hyaline awn, and rather than on soil, it occurs on exposed dry volcanic rock.

Fissidens sublimbatus Grout [Fissidentaceae]

Only two genera of mosses recorded from the Santa Monica Mountains have leaves in one plane, *Fissidens* and *Bryolawtonia*, the later of which is much branched and rare in the region. Along with having flat shoots, *Fissidens* has leaves laid out like those of an iris, and the leaves have two lamina of different sizes (dorsal and ventral) fused together along the midrib, forming a pocket that clasps the stem. Three species of *Fissidens* are known from the Santa Monica Mountains; all of them occur in moist habitats, mainly on soil, but sometimes on rock, and *Fissidens crispus* has been found on loose gravelly soil submerged in a seasonal trickle. Common and abundant anywhere in the range where moisture is available, *Fissidens* is often the first species to colonize a shaded trailcut. By far the most common *Fissidens* in the range is *Fissidens sublimbatus*. Its dorsal lamina tapers to extinction before it reaches the midrib. It is also a plant of drier habitats than either *Fissidens bryoides* or *Fissidens crispus*.
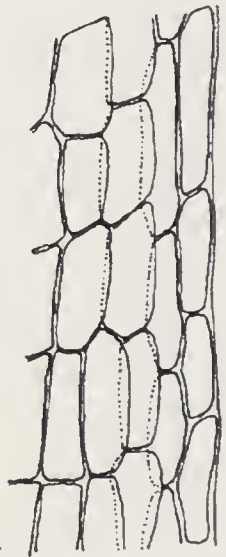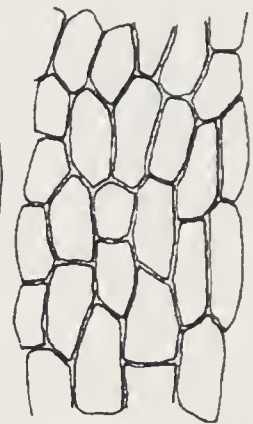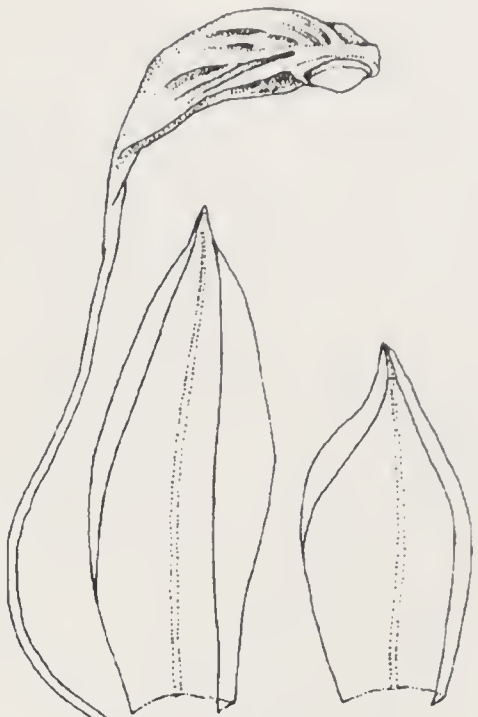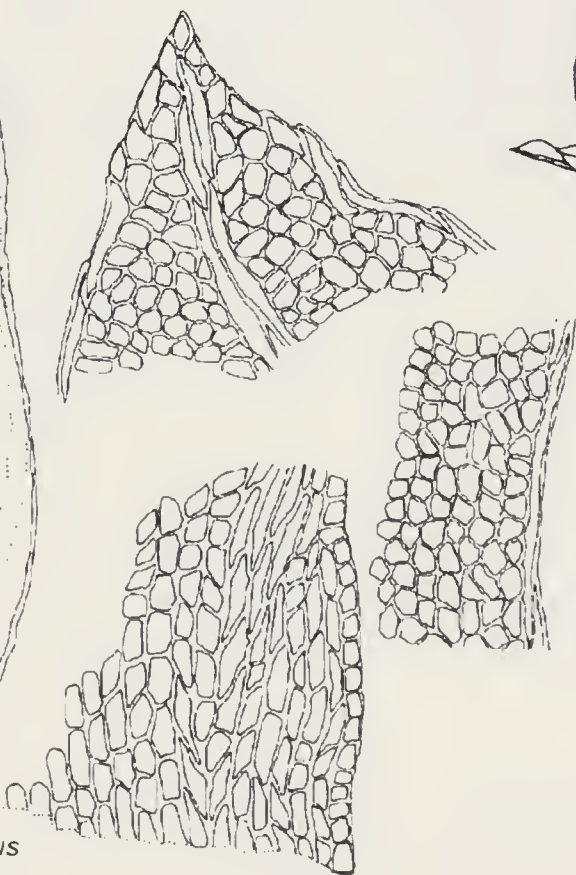
Funaria hygrometrica Hedwig [Funariaceae]

Out of the six North American genera in the family Funariaceae, only *Funaria* has been reported from the Santa Monica Mountains, but at least *Entosthodon bolanderi* has also been collected in southern California and along much of the California coast ranges and could occur here. *Funaria hygrometrica* is a globally common species in disturbed areas, along roadsides, ditches, trail edges, and in openings in woodlands and coastal scrub. It is an acrocarpous moss with individual plants visible with the naked eye, and it produces copious sporophytes with strongly curved, twisted setae, and capsules that are widest near the mouth. The orange coloring of the capsules and setae are also highly diagnostic. It is furthermore quickly recognized for its asymmetric capsule that has a dome-shaped operculum set at a diagonal, a feature that separates it from all other local mosses including the much smaller and much less common *Funaria muhlenbergii*.

Aloina
rigida
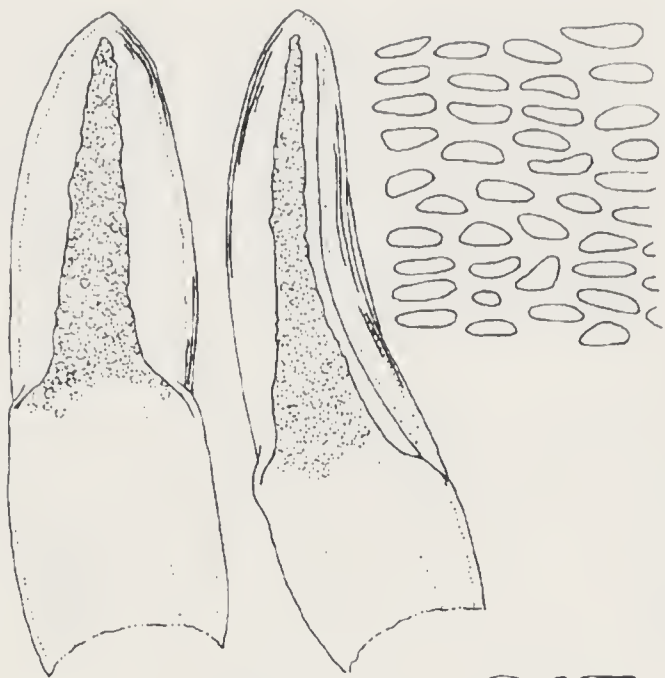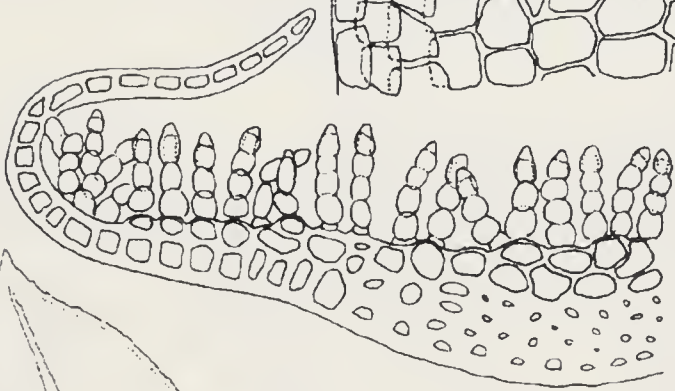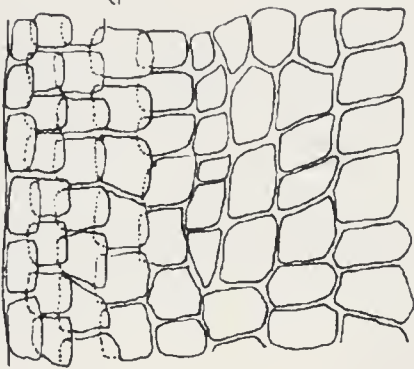
Funaria
hygrometrica

Fissidens sublimbatus

Plate 2: Acrocarps

Encalypta rhaptocarpa Schwägrichen [Encalyptaceae]

Out of eight species of *Encalypta* in California, only one, *Encalypta rhaptocarpa*, has been found in the Santa Monica Mountains, where it occurs on thin soil over exposed volcanic rock. This small acrocarpous moss commonly bears sporophytes donned with a pointed calyptra large enough to fully cover the capsule, making it easy to recognize. However, to identify a specimen to a species, a compound scope is necessary to see such minute characteristics as papillosity and coloration of the cell walls.

Bryum capillare Hedwig [Bryaceae]

Bryum are minute to robust acrocarpous mosses with rather large hexagonal to rectangular thin-walled cells, and sporophytes with pendant to horizontal, mostly long pear-shaped capsules. There are several more *Bryum* species in the Santa Monica Mountains than have been identified to date. *Bryum capillare* plants are dark green to brownish above and brown to reddish below. They form loose to rather dense patches, and are often mixed in with other mosses. The species is perhaps easier recognized in its dry state when the leaves twist spirally around the stem so that a patch of plants consists of contorted little knobs. *Bryum capillare* leaves are usually crowded in the median and upper part of the stems. They are oblong to ovate, narrowed at base, somewhat concave, nearly entire, and sometimes with a hint of crenulate edge toward the tip. *Bryum capillare* is a disturbance-oriented cosmopolitan species that occurs on soil and rock, on cement walls, at bases of trees, and in pockets of dirt in rock outcrops along seasonal drainages.

Bryoerythrophyllum ferruginascens (Stirt.) Giac. [Pottiaceae]

Bryoerythrophyllum are acrocarpous mosses with lanceolate leaves that have rounded to narrowly obtuse tips, and entire plane leaf margins above the mid leaf. The genus is reminiscent of *Barbula, Didymodon* and *Pseudocrossidium* not only in its leaf morphology, but also in having papillose, isodiametric cells. *Pseudocrossidium* leaves, however, are extremely recurved with the margin turning under a full spiral. Unlike the other above-mentioned genera, *Bryoerythrophyllum* has reddish coloration. Three *Bryoerythrophyllum* species have been reported from the Santa Monica Mountains. Superficially, *Bryoerythrophyllum ferruginascens* resembles *Amphidium mougeotii*, a species not yet reported from the southern California, and a translucent pale yellow-green coloration would give *Amphidium mougeotii* away. *Bryoerythrophyllum ferruginascens* could also be confused with some of the *Didymodon* species, but closer examination under a compound scope would reveal solid papillae in *Didymodon*, while *Bryoerythrophyllum* papillae are hollow. In the Santa Monica Mountains, *Bryoerythrophyllum ferruginascens* grows on volcanic rock in seasonal drainages and forms rather dense turfs that are bright green when wet and reddish brown when dry. During the winter months, this moss is often saturated in running water. Nearly circumarctic, *Bryoerythrophyllum ferruginascens* is known from northern Asia, Alaska, Greenland, the Appalachians, the Rocky Mountains, central mainland Mexico south to Veracruz, Bolivia, parts of Africa, Europe, Philippines, and New Guinea (Zander 2006). It appears to be widespread although with only infrequent occurrences. This is the first report of it from California.

Phascum cuspidatum Hedwig [Pottiaceae]

This extremely small moss is gregarious or scattered. *Phascum cuspidatum*, with its ovate to oblong-lanceolate leaves reaching over the sporophyte hiding the capsule from view, is rarely found without sporophytes. The tiny moss occurs only in the spring on dry soil among grasses, under shrubs, or sometimes in open places.
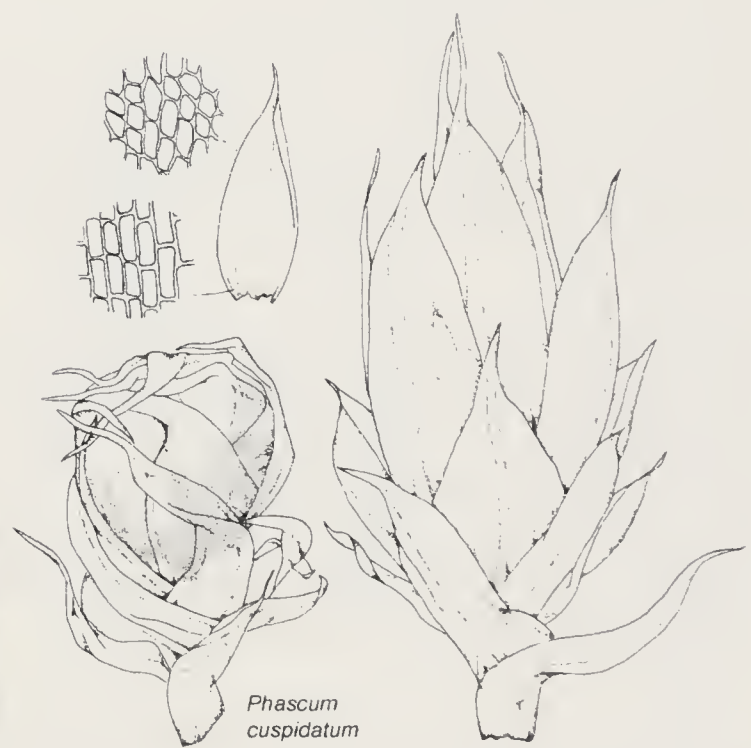
Encalypta rhaptocarpa

Bryum capilare

Bryoerythrophyllum ferruginascens

Phascum
cuspidatum

Plate 3: Acrocarps

Timmiella anomala (Bruch *in* W. P. Schimper) Limpricht [Pottiaceae]

    Timmiella is a common upright somewhat weedy moss of trail edges, creek banks, and other areas of minor to moderate disturbance. It can occur as scattered individuals or more dense patches on seasonally moist soil and it is often mixed with other mosses such as species of *Didymodon, Bryum,* and *Weissia* that also do well in the areas of some disturbance. *Timmiella* is one of the larger acrocarpous mosses on soil in the Santa Monica Mountains, and is easily identified in the field for its thick apple-green lanceolate leaves with an incurved margin when wet, and for its contorted coiled habit that leaves the broad midrib visible at the back of the curled up leaf when dry. With sporophytes generally lacking, it is difficult to separate the two *Timmiella* species found in California, but based on a few collections of plants with sporophytes, it appears that *Timmiella crassinervis* prefers the more humid north, while *Timmiella anomala* tends to be found in the drier south (Norris and Shevock 2004).

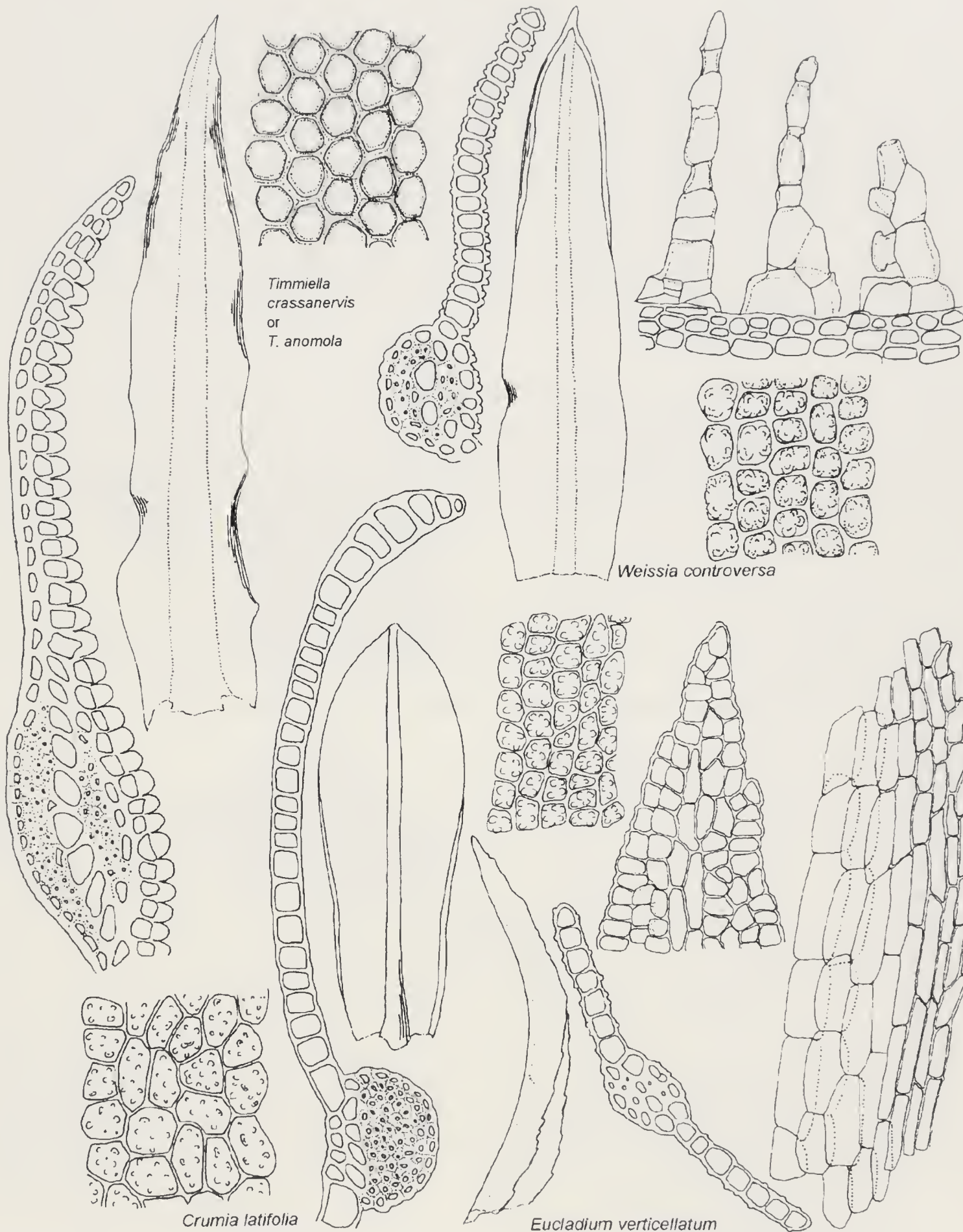*Weissia controversa* Hedwig [Pottiaceae]

    Weissia is often collected unintentionally, mixed in with *Timmiella* or other soil mosses, and in its dry state, it looks like a tiny version of *Timmiella*. When dry, the leaves of both species are strongly incurved and contorted. Both species have narrowly lanceolate leaves, but *Weissia* leaves are also broadly channeled when they are wet, and the midrib extends just beyond the leaf point to form a small mucro, a feature not present in *Timmiella*. A rather common moss with nearly worldwide distribution, *Weissia controversa* is easily overlooked for its small size and quick life cycle, occurring late in the season for most local bryophyte activity. This species is known to favor calcareous substrates but it is not restricted to them, and like other *Weissia* species, it does well along trail sides and other areas of disturbance.

Crumia latifolia (Kindberg) W. B. Schofield [Pottiaceae]

    Although not abundant in the Santa Monica Mountains, the monotypic dark green *Crumia latifolia*, endemic to the west coast of North America, can be found in many of the creeks and waterfall areas on wet calcareous rock faces or seeps, sometimes in a continuous trickle of water. The species has broad, tongue-shaped leaves reminiscent of some *Tortula* and *Syntrichia* species but it occurs in much wetter, more shaded habitats and the darker colored border of the leaves is highly diagnostic.

Eucladium verticillatum (Hedwig *in* Bridel) Bruch & W. P. Schimper [Pottiaceae]

    Only one *Eucladium* species is known from the southwestern United States. The plants form lime encrusted, lumpy tufts and extensive cushions on usually calcareous substrates along edges of waterfalls, and on rocks with seeps and creek splash. This moss occurs in the Santa Monica Mountains in most of the major drainages and is easily recognized for its habit and dark green coloration. *Eucladium verticillatum* leaves are long and narrow, with flat crenulate margins, and strongly papillose which makes the leaf opaque. In the Santa Monica Mountains, the species could be confused with *Didymodon tophaceous*, which has a similar morphology and can occur in the same location or near by. *Didymodon tophaceous*, however, lacks the mucro (a clear cell that forms a short point) at the tip of the *Eucladium* leaf as well as the few teeth at the base of the leaf typical to *Eucladium*.

Timmiella
crassanervis
or
T. anomola

Weissia controversa

Crumia latifolia

Eucladium verticellatum

Plate 4: Acrocarps

Syntrichia princeps (De Notaris) Mitten [Pottiaceae]

Syntrichia bears many similarities with *Tortula*, from which it was recently segregated. Both have broad, tongue-shaped, densely papillose leaves that often bear hair-points, and both commonly have a sporophyte that has a long, twisted peristome (teeth lining the mouth of the capsule). Although only the two most common *Syntrichia* species, *S. princeps* and *S. ruralis*, have been so far observed from the Santa Monica Mountains, many others could occur in the range because the genus is thought of as being particularly well adapted to mediterranean climate conditions. All local *Syntrichia* have a hyaline awn present at least on some leaves, and the leaf lamina is composed of two layers of cells only at the margins or apex if at all. *Syntrichia princeps* seems to prefer dry rock in the Santa Monica Mountains. It has a leaf margin that is recurved nearly to the apex, and a rigid awn crowded with teeth and often reddish-brown near the base. *Syntrichia ruralis* is a generalist species that does not have very specific habitat requirements.

*Gymnostomum calcareum* Nees & Hornschuch [Pottiaceae]

Although elsewhere *Gymnostomum* is known to form dense large cushions, the few populations known from the Santa Monica Mountains are only somewhat dense patches along shady crevices of a volcanic rock outcrop, on a side of a sandstone boulder, and on a damp shaded side of a ditch. Most of the known locations have calcareous seeps, but they are dryer than *Gymnostomum* habitat elsewhere in California. Morphologically the species could possibly be confused with *Eucladium verticillatum* and some of the *Didymodon* species of calcareous substrates that have lanceolate papillose leaves. The olive-green *Gymnostomum*, however, is at least in our range much shorter than the species mentioned above. It lacks the teeth usually present at the base of the leaf in *Eucladium verticillatum*, and unlike *Didymodon*, *Gymnostomum* lacks peristome teeth on the rim of its capsule.

*Tortula atrovirens* (J. E. Smith) Lindberg [Pottiaceae]

Tortula are small plants with mostly simple stems or with few branches. A long spiraling peristome consisting of filiform divisions is characteristic of the genus, although it is reduced in some species. The plants have broad, spatulate or tongue-like, usually ovate to elliptic or obovate leaves that are twisted when dry, and upright spreading to squarrose when moist. The tip of the leaf is acute in some of the *Tortula* species, rather blunt in others, and in some the leaves have hair-points that give the tufts of plants a frosty look. *Tortula atrovirens*, formerly in the now unavailable genus *Desmatodon*, and *T. bolanderi*, not yet reported from the Santa Monica Mountains, are two of the few *Tortula* in southern California that consistently do not have a hyaline leaf point. Furthermore, it differs from the other southwest *Tortula* in that it has a thick cushion of enlarged cells on the ventral surface of the midrib at the upper portion of the leaf near the tip of the leaf, making the midrib convex or bulging. The plants are green above, tan below, and often have reddish leaf tips. *Tortula atrovirens* favors exposed calcareous soil and crumbly rock.

*Didymodon vinealis* (Bridel) Zander [Pottiaceae]

As with California as a whole, *Didymodon* in the Santa Monica Mountains is one of the most common and most diverse of moss genera. Several *Didymodon* species have been reported from the range, along with other similar species with lanceolate leaves that have densely papillose quadrate cells and entire, often somewhat recurved margins. Green to dark-green, or occasionally red- to yellowish-brown, this member of a difficult genus with varying habitat preferences has the look of an archetypal upright moss, and can form considerable patches on rocks, along creek banks, and trail cuts.
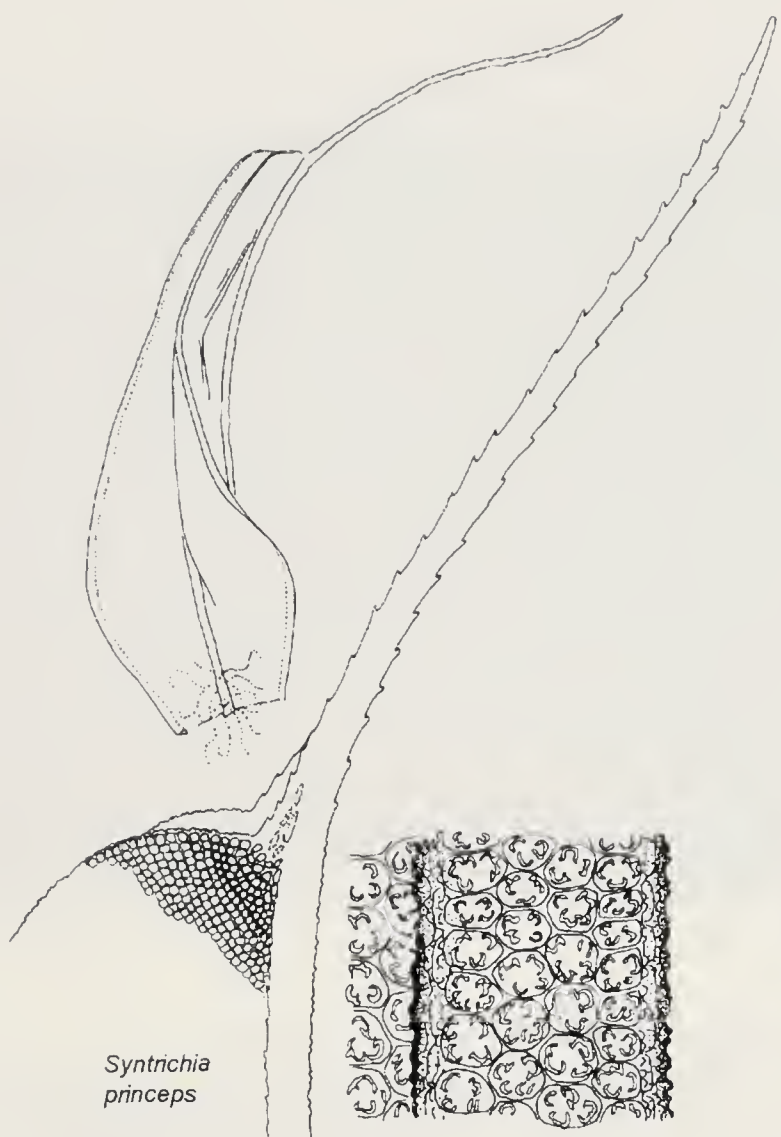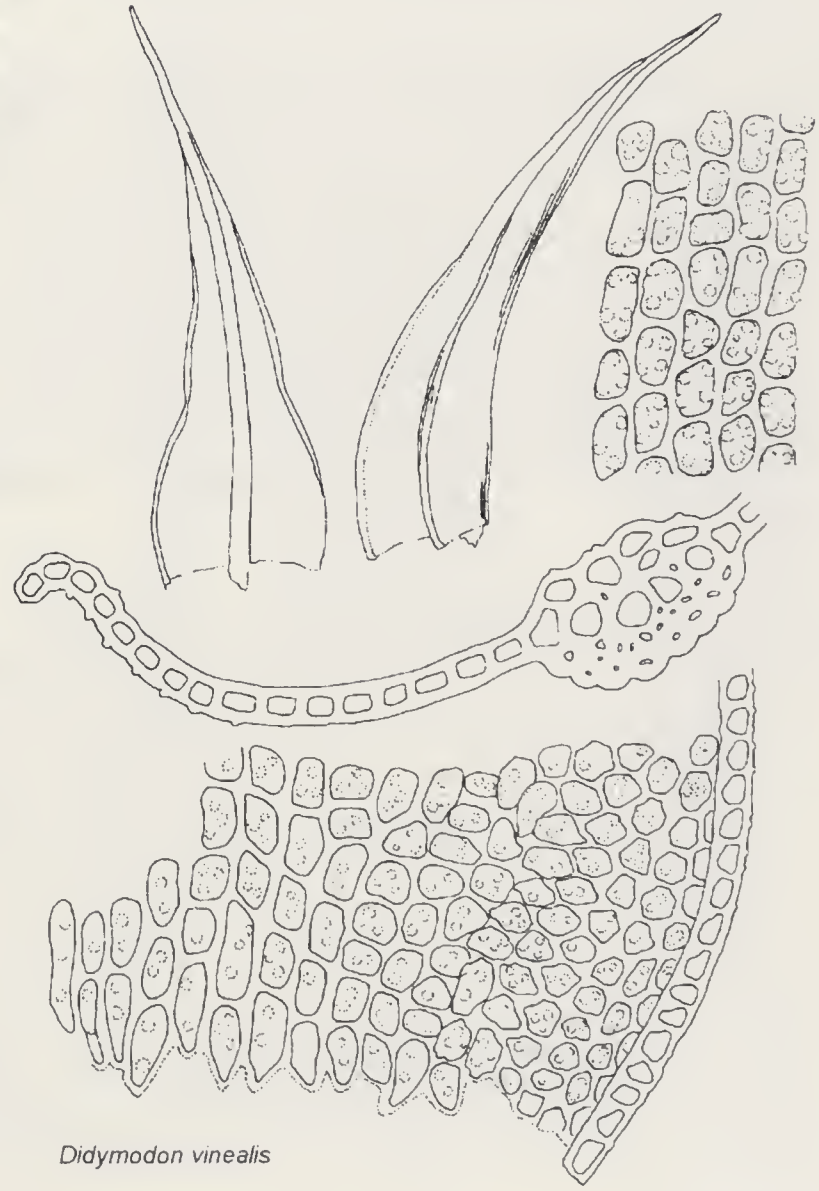
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princeps
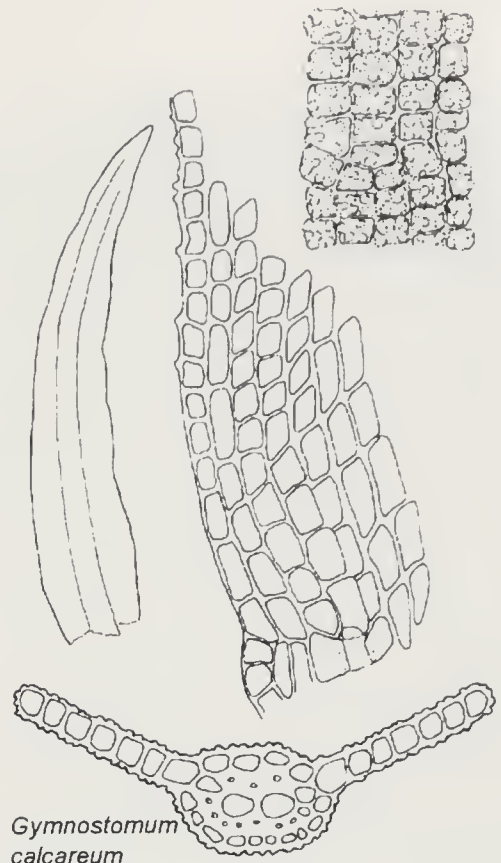
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calcareum
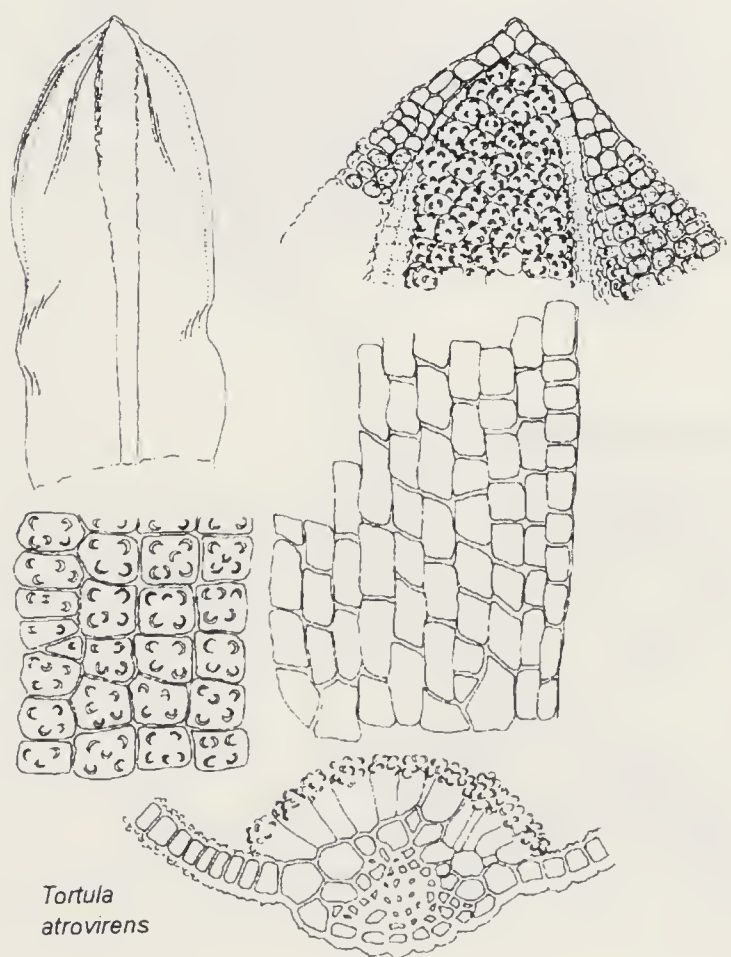
Tortula
atrovirens

Didymodon vinealis

Plate 5: Acrocarps

Grimmia lisae De Notaris [Grimmiaceae]

Grimmia is a notoriously difficult genus. Out of the 36 reported for California, at least five occur in the Santa Monica Mountains where the genus is the most common moss on rock. Most *Grimmia* prefer temperate parts of the world, and nearly half of the species have restricted distributions. Yet, a single rock outcrop can host several *Grimmia* species. In the Santa Monica Mountains, *Grimmia* is well distributed across the landscape in various habitats. It occurs on rock outcrops in chaparral, riparian areas, woodlands, and on open, exposed outcrops. Although *Grimmia* typically may have many phenotypes depending on particular environmental conditions, with sufficient patience one can come to terms with the local species. *Grimmia lisae* is the most common *Grimmia* in the Santa Monica Mountains. The species forms loose dark green tufts on generally north facing, shaded boulders that may be exposed part of the day. When moist, *Grimmia lisae* leaves twist open making the plants look like patches of miniature pinwheels; when dry, the leaves are erect and appressed. This species has a highly variable leaf tip ranging from no hair-point to one that is rather long, stout, and denticulate. Its leaf margin also varies from being recurved on only one side to being recurved on both sides. In profile, the leaf midrib of *G. lisae* forms an outward tending arc rather than the mild S-shape typical of *Grimmia trichophylla*, the other common *Grimmia* species in the Santa Monica Mountains.

Schistidium cinclidodonteum (C. Müller Hal. *in* Röll) B. Bremer [Grimmiaceae]

In the past, *Schistidium* was included in *Grimmia*, and it shares morphological similarities with it, such as its lanceolate to ovate-lanceolate leaves. In the field, *Schistidium* can be readily recognized from *Grimmia* for its dark reddish brown coloration, habit of loose cushions, immersed capsules, and occurrence in seasonal creeks and seepages. *Schistidium* can be found on open bedrock in areas where other species would prefer cracks with at least some soil. Only one, *Schistidium cinclidodonteum*, out of ten known *Schistidium* species in California have been found in the relatively low elevation Santa Monica Mountains. The species occurs in intermittent seepages on exposed bedrock in the highest elevation areas of the range.

Anacolia menziesii (Turner) Paris [Bartramiaceae]

Anacolia forms palm-sized and larger, moderately dense tufted patches in crevices and small shelves with a little soil, on both sandstone and volcanic rock outcrops. It occurs throughout the Santa Monica Mountains and it is easily recognized for its red-brown rhizoids that coat the lower portions of the stem. Out of the three species in California, two are known from the range, *Anacolia baueri* and *Anacolia menziesii*. The best way to tell them apart is the shape of the capsule, which is oblong to short-cylindric in *Anacolia baueri* and nearly round in *Anacolia menziesii*. Unfortunately, *Anacolia* rarely has sporophytes in the Santa Monica Mountains. However, the characteristic habit of the species has been found to be consistent. In dry condition, *Anacolia baueri* branches form a tight cluster where all leaf tips are closely parallel pointing to one direction, while in the *Anacolia menziesii* the leaf clusters at the branch tips tend to diverge in all directions, giving the moss patches a slightly roughed-up appearance.

Grimmia lisae

Schistidium
cinclidodonteum

Anacolia
menziesii

Plate 6: Acrocarps

Orthotrichum tenellum Bruch ex Bridel [Orthotrichaceae]

In the Santa Monica Mountains, *Orthotrichum* is one of the few mosses that occur on trees—mainly on oak and sometimes on large willows. They are never plentiful in the semi-arid conditions of the range, yet *Orthotrichum* is relatively species-rich among our genera. Even so, only six out of the 31 species reported for California occur here. *Orthotrichum* are dark green scattered tufts in bark crevices of course bark and on rock, depending on the species. In Northern California, the plants can grow quite large and produce considerable branching, but the plants in our mountains are only little branched and mostly quite small. The ovate-lanceolate to oblong lanceolate leaves are generally crowded and often contorted when dry. They are mostly acute, usually keeled, and mostly with an entire margin. *Orthotrichum* species commonly have sporophytes available, which is fortunate because many of the characteristics used to identify *Orthotrichum* to species are sporophytic. In many cases, a compound scope is necessary to look at these characteristics, but several larger characteristics can be helpful, such as the position of the capsules in respect to the surrounding perichaetial leaves. Furthermore, the capsules can be broadly ovoid to oblong-cylindric, sometimes pear-shaped, and often ribbed. *Orthotrichum tenellum* grows in light- to dark-green tufts on bark. It has small, blunt, stiffly erect leaves, and a naked (or sparsely hairy) calyptra (cap-like covering) nearly covering the capsule. *Orthotrichum rupestre* is the most common species found on rocks.

Leptobryum pyriforme (Hedwig) Wilson [Meesiaceae]

From some distance, this moss appears as a patch of light-green fuzz. The nearly unbranched plants with long, narrow leaves form dense tufts on soil along moist creek banks, in a seep on shaded sandstone outcrop, old burn sites, or other disturbed areas. One might possibly confuse the morphology of a few itinerant plants with *Ditrichum*, but the latter is smaller, and it will not form extensive dense patches clearly visible to naked eye. *Leptobryum pyriforme*, the only species in the genus, commonly has sporophytes with pendent pear-shaped capsules reminiscent of many *Bryum* and *Pohlia* species. Only occasional in the Santa Monica Mountains, the species has been observed along Zuma Creek and on calcareous seep in a shaded sandstone outcrop in the central range. This moss has nearly a worldwide distribution, ranging from the Arctic to New Guinea.

*Hedwigia detonsa* (Howe) W. R. Buck & Norris [Hedwigiaceae]

Hedwigia form loosely arranged small patches of grey-green creeping plants on volcanic rock in the central and western portions of the range. The plants have concave papillose leaves with long hairpoints that give the patches a hoary appearance. Usually the plants are mixed in with other mosses, commonly with various *Grimmia* species. *Hedwigia* is more tolerant of open habitats than most mosses, frequently remaining completely exposed, although generally, nevertheless, on northerly facing slopes of the boulders and ridgelines. Besides the distinctive habit and environment, the irregularly branched papillae further confirm the identity of the species under a compound scope. Out of the three *Hedwigia* species known from California, only *Hedwigia detonsa* has been confirmed for the Santa Monica Mountains. It has consistently only 1-2 papillae on the upper laminal cells, and the awns of the vegetative leaves have spines.
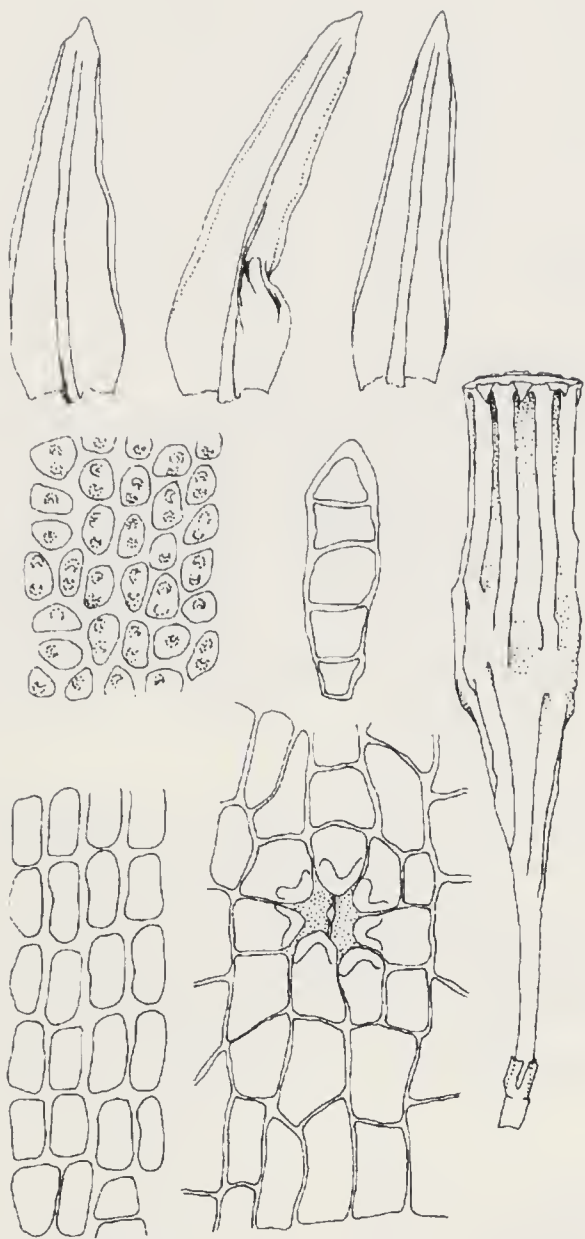
Orthotrichum tenellum

Leptobryum pyriforme
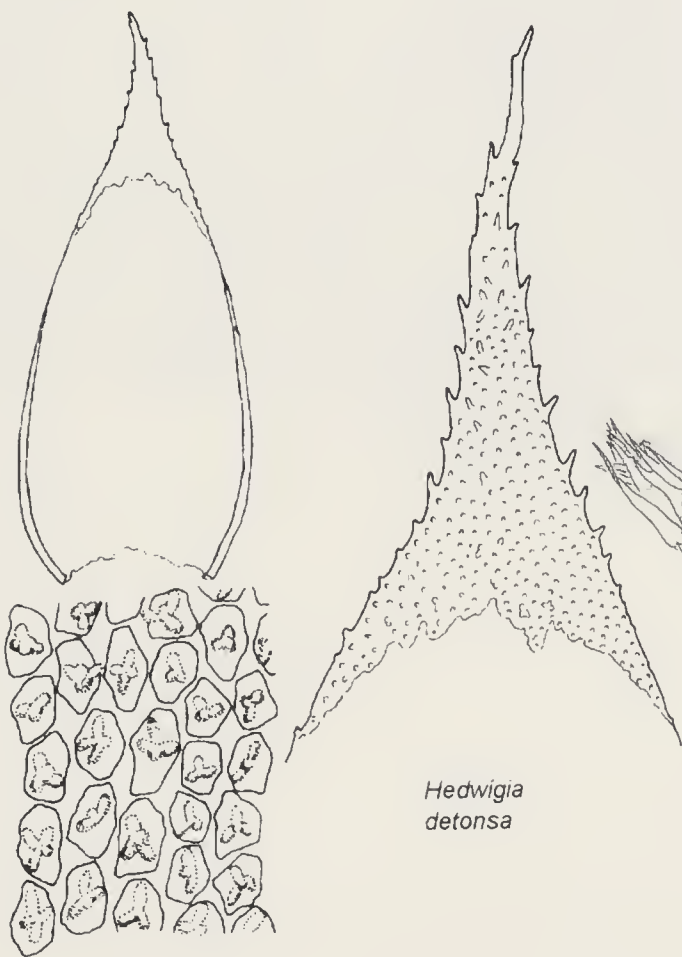
Hedwigia detonsa

Plate 7: Pleurocarpous (prostrate branching) mosses

*Bryolawtonia vancouveriensis* (Kindberg) Norris & Enroth [Neckeraceae]
This mainly northern California species is presently known only from one location in the Santa Monica Mountains, in upper Carlisle Canyon, where it forms a thin mat on an underhang of volcanic rock in a deeply shaded seasonal drainage. This very small prostate moss has a flattened look resulting from spirally inserted twisted leaves. The complanate appearance together with the rounded leaf tips could lead one to think the species is a leafy liverwort, but a closer examination will reveal a midrib, a character not present in liverworts.

*Pterogonium gracile* (Hedwig) J. E. Smith [Leucodontaceae]
Pterogonium gracile forms patches of up to 2-3 square feet, but it can also occur as scattered tufts and individuals mixed in with other mosses. In the field, this species could be confused with *Antitrichia californica* for its somewhat claw-like appearance in its dry state, but the latter forms looser patches, and the plants have a yellowish green cast, while *Pterogonium gracile* plants are muted grayish green. There are only a few sparse *Antitrichia californica* occurrences in the Santa Monicas, and most of these locations are more dry and exposed than typical *Pterogonium gracile* habitat.

Dendroalsia abietina (W. J. Hooker) E. Britton *in* Brotherus [Cryphaeaceae]
Dendroalsia abietina is endemic to the west coast of North America, and in northern California it is one of the most conspicuous mosses covering tree trunks. The Santa Monica Mountains represent nearly the southern limit for this species, which ranges from northern Mexico (where it is known only from Guadalupe Island) to British Columbia and inland to Idaho. In the Santa Monica Mountains, this species is presently known from two shaded north facing volcanic outcrops, in upper Carlisle Canyon and at the Goat Buttes near Century Lake. Due to its large size and distinctive habit, monotypic *Dendroalsia abietina* is easy to recognize. The dry plants curl down in a distinctive manner, and when wet, they appear flat like a feather perpendicular to the rock face (or tree trunk in northern California). Paraphyllia, leaf-like structures cloaking the branches under the true leaves, are common in this species, but lacking in both *Bestia longipes* and *Pterogonium gracile*.
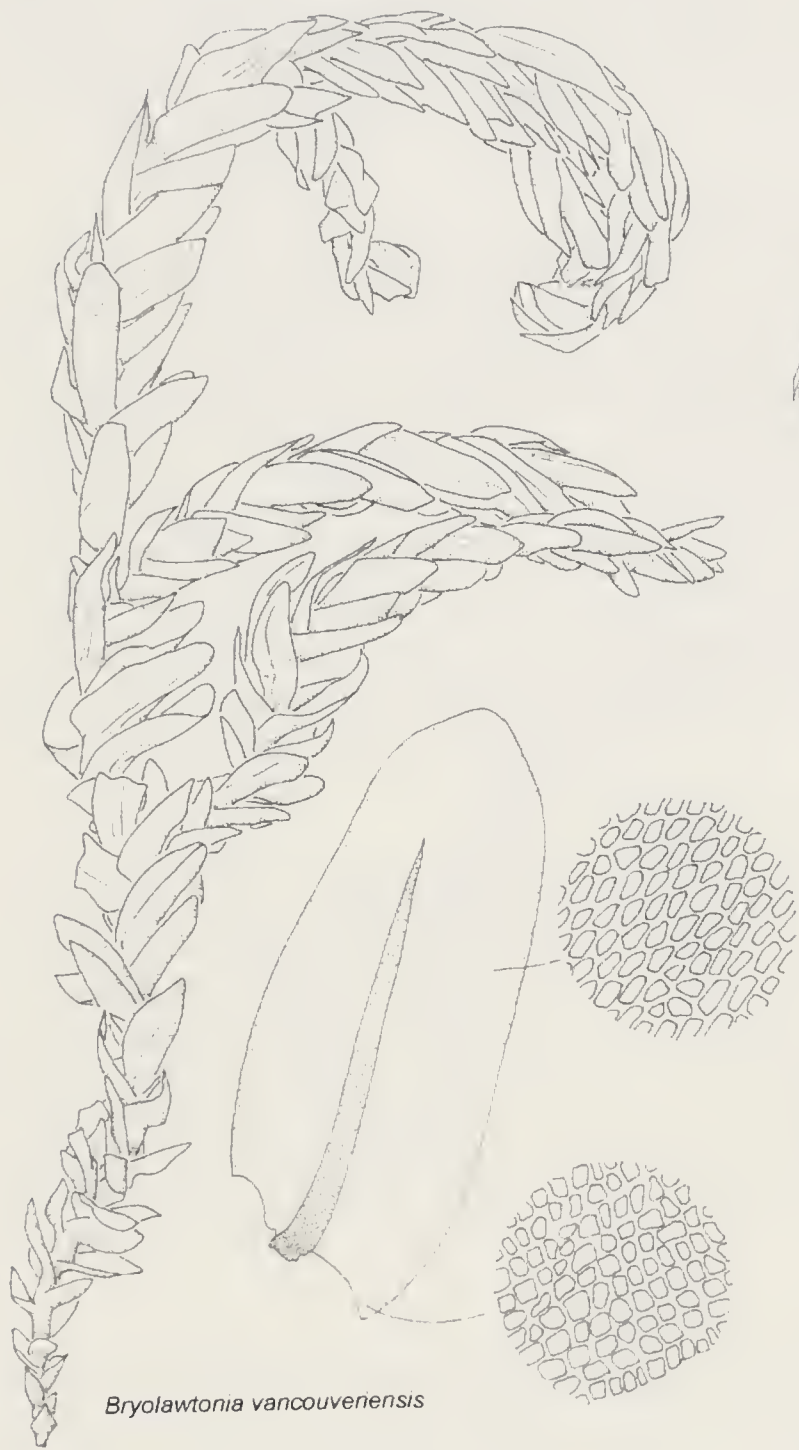
Pterogonium
gracile

Bryolawtonia vancouvenensis
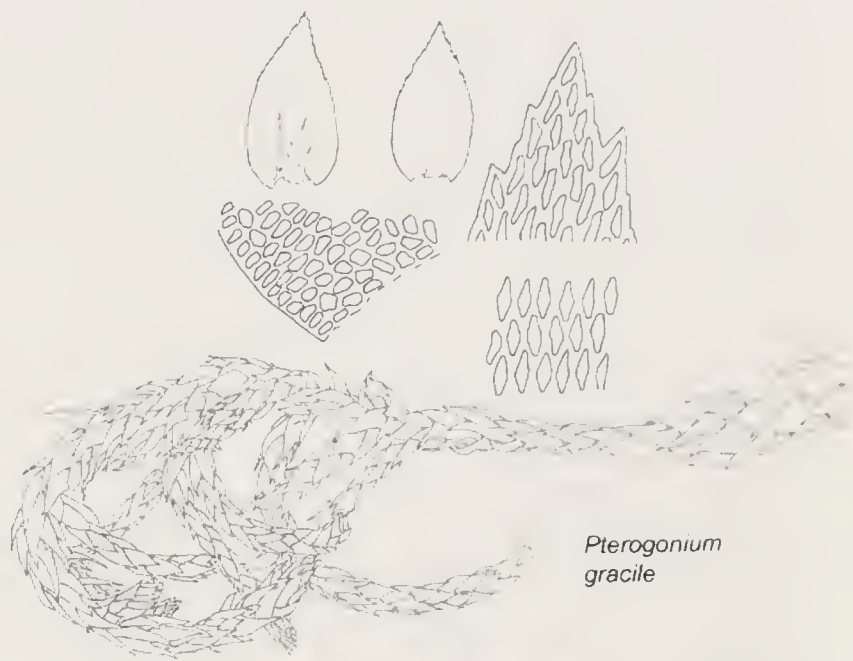
Dendroalsia abietina

Plate 8: Pleurocarps

Amblystegium juratzkanum W. P. Schimper [Amblystegiaceae]

Amblystegium are small, creeping, irregularly branched mosses of wet places. Not very common in the Santa Monica Mountains, they can be found now and then on wet creek banks or submerged in seasonal flow. Their leaves are ovate to lanceolate with an acuminate tip and plane, serrulate (sometimes entire) margins, and a slender midrib extending nearly to mid-leaf. *Amblystegium* could be confused with *Brachythecium bolanderi*, but the latter tends to occur a little higher up on the creek bank on damp to moist soil or between tree roots. *Brachythecium bolanderi* leaf margins are more strongly serrate than those in *Amblystegium*; they are serrate nearly to the base. The two *Amblystegium* species in the range can be told apart by the degree of spreading of the leaves: *Amblystegium juratzkanum* leaves are wide-spreading whether they are wet or dry, whereas *Amblystegium serpens* leaves are more or less erect when dry.

*Leptodictyum riparium* (Hedwig) Warnstorf [Amblystegiaceae]

Leptodictyum are slender to moderately robust creeping mosses that occur in thin mats in moist or wet places, in filtered light along riparian corridors. Their leaves are spreading, oblong-lanceolate, with an acuminate tip, and the cells are smooth. Leaf margins are plane and entire or nearly so. The slender midrib ends at or just above the leaf middle, below the acumen. There are two *Leptodictyum* species in Santa Monica Mountains. *Leptodictyum riparium* has a midrib that is short, ending well below the acumen and the asymmetric leaves are, at least on some stems, inserted somewhat obliquely. *Leptodictyum humile* leaves are symmetric and they are attached to the stem transversely. The two species often occur in the same drainage but in different microhabitats. *Leptodictyum riparium* favors slow-moving or stagnant water where it is often found completely submerged seasonally, whereas *Leptodictyum humile* is usually found on moist soil or tree roots along the creek bank.

Claopodium whippleanum (Sullivant) Renauld & Cardot [Leskeaceae]

Only one *Claopodium* species is found in the Santa Monica Mountains. The other two Californian *Claopodium* species (*Claopodium crispifolium and Claopodium bolanderi*) are known from the Sierra Nevada and north coast conifer forests. They are not likely to occur in our semi-arid chaparral and oak woodland conditions. *Claopodium whippleanum* is a small green to golden-green creeping moss on moist soil. Although it forms only lackluster patches in the Santa Monica Mountains, it is relatively frequent throughout the range in the more mesic drainages. When dry, *Claopodium* is easily recognized under a hand lens for its chain-link appearance.

Conardia compacta (C. Muller Hal.) H. Robinson [Campyliaceae]

Conardia compacta, a monotypic genus, is reminiscent of *Amblystegium* and *Leptodictyum* in being a small creeping moss on soil of moist habitats. Unlike the other two, *Conardia compacta*, however, tends to favor calcareous and alkaline substrates. *Conardia compacta* has crowded, erect to erect-spreading, lanceolate to ovate-lanceolate, decurrent leaves and double teeth at the edge of the leaf base at least in some leaves. The plants commonly bear filamentous propagula at the back of the leaves above the middle. If a compound scope is available, *Conardia compacta* will prove to have papillose rhizoids, while other similar local mosses have smooth rhizoids.
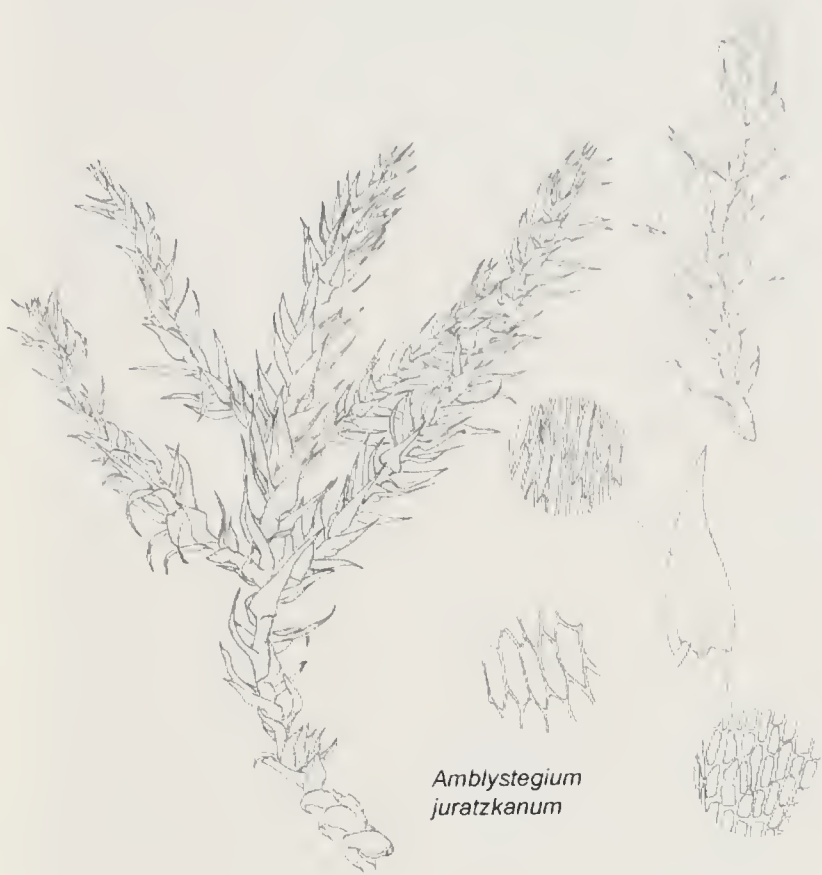
Amblystegium
juratzkanum

Leptodictyum riparium

Claopodium whippleanum

Conardia
compacta

Plate 9: Pleurocarp

Bestia longipes (Sullivant & Lesquereux) Brotherus [Brachytheciaceae]
    The monotypic *Bestia longipes* occurs on both volcanic and sandstone rock in shaded riparian
    drainages. The stem leaves and the branch leaves are similar: blunt or obtuse, obscurely
    plicate, ovate-lanceolate, and with an acute tip. The margins are recurved in the lower 2/3 and
    serrate at the apex. The stout midrib extends up to the leaf tip. The thick-walled cells are
    rhombic and their projecting ends appear as scattered spines on the back of the leaf. *Bestia*
    occurs often near by *Pterogonium gracile* in shaded narrow drainages but it tends to occupy
    slightly moister, more shaded parts of the same boulder or rock face. The species is common
    along the central California coast and endemic to only a somewhat larger region. The
    opposing photographs show *B. longipes* wet (above) and dry (below).
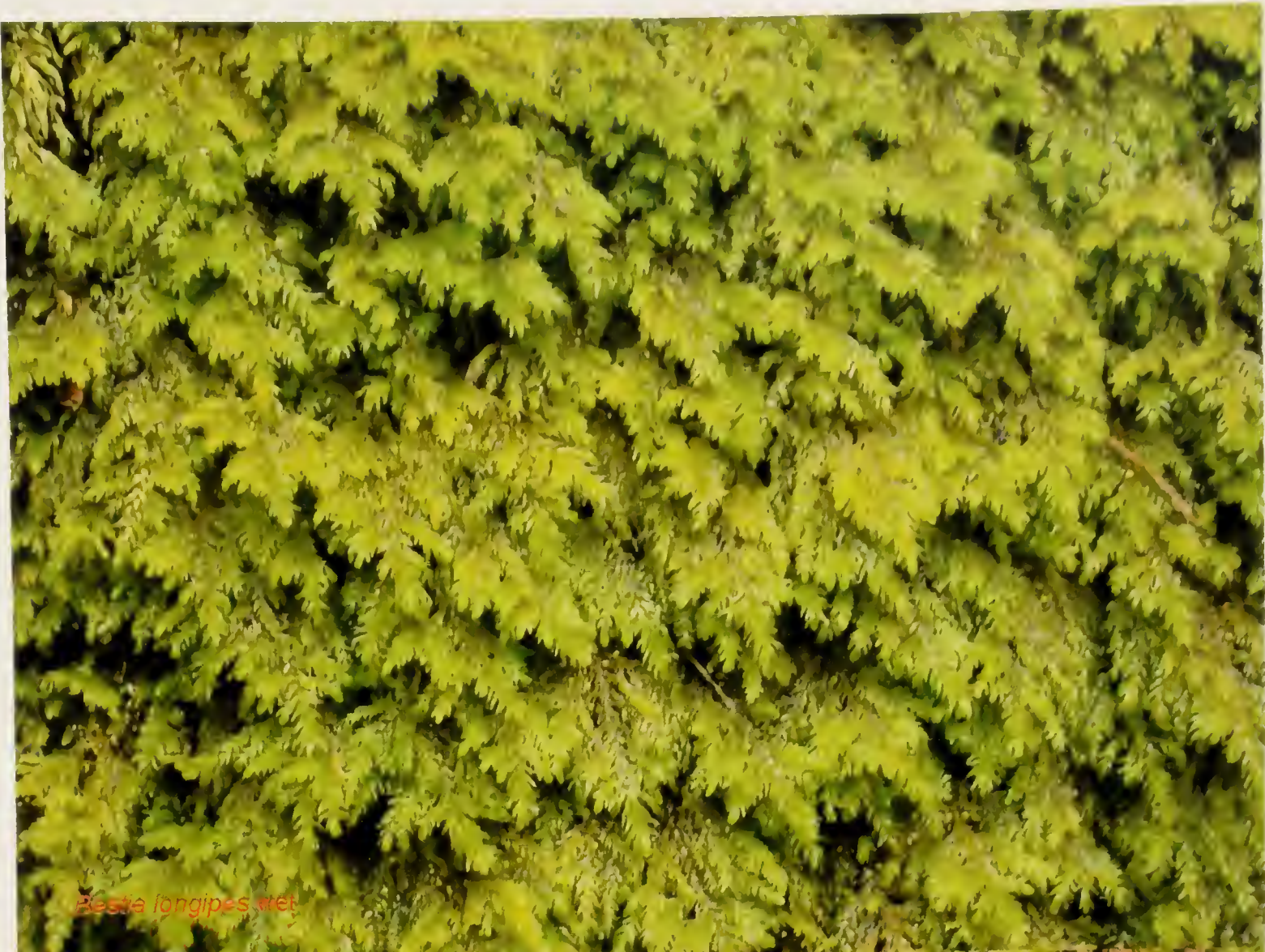
Bestia longipes.wet

Bestia longipes.dry

Plate 10: Pleurocarps

Homalothecium pinnatifidum (Sullivant & Lesquereux) E. Lawton [Brachytheciaceae]
   Most *Homalothecium* are distinctively pinnate with short regular golden branches that twist upward. The exception is the more stringy *Homalothecium arenarium*. *Homalothecium's* leaf shape varies from lanceolate to elongate triangular, and has strong plicae at the concave base. Through a compound scope one can detect a series of spines on the midrib. This feature that is particularly helpful with *H. arenarium*, which has several spines closely arranged at the tip of the midrib while the spines in the others are inconspicuous and mostly single. Dry *H. pinnatifidum* branches are markedly hook shaped with plants loosely attached to rock faces. In general, *Homalothecium* species tend to prefer drier sites than our *Brachythecium* species which can range from seasonally submerged to mesic to somewhat dry sites.

Scleropodium touretii (Bridel) L. Koch [Brachytheciaceae]
   Scleropodium are prostrate creeping mosses forming glossy shag that lays flat and downwardly pointing over rock or soil. The tight rope-like branches are telltale for the genus. Furthermore, the plants have smooth, broadly ovate to ovate-lanceolate, concave leaves that have plane, entire to serrulate edges. *Scleropodium* is perhaps the most common pleurocarpous moss in the Santa Monica Mountains, well distributed through out the range. Out of the six California species, all but one (*Scleropodium colpophyllum*) have been reported from the range. *Scleropodium touretii* is one of the larger *Scleropodium* species in the Santa Monica Mountains with only *Scleropodium obtusifolium* being sometimes larger. *Scleropodium touretii* forms lush thick patches, mainly on soil and not generally submerged, and tend to be rather uniform with all the branches having a strongly rope-like appearance. At least some stems have leaves with a short-acuminate tip curving outward away from the stem. *Scleropodium obtusifolium* grows in places that are seasonally submerged. The other smaller species are more likely to be on rocks in shady areas.

Brachythecium albicans (Hedwig) Bruch & W. P. Schimper [Brachytheciaceae]
   Brachythecium are prostrate and mostly mesophilic. Although the genus is difficult worldwide, our four *Brachythecium* species (*Brachythecium albicans*, *B. asperrimum*, *B. bolanderi*, and *B. velutinum*) are fairly distinctive. When wet, *Homalothecium* (especially *Homalothecium arenarium*) could be confused with *Brachythecium*. *Brachythecium albicans*, like other *Brachythecium* species in the range, has a midrib that usually ends at 1/2 to 3/4 of the leaf length, but it is the only one with the plicae extending up at least 1/4 of the leaf length. The others have no plicae, or the plicae are restricted to the leaf base. *Brachythecium albicans* leaves are narrow to linear, they have a nearly entire awn, and when the leaves are dry, they overlap closely in an orderly manner. The other very common species, *Brachythecium bolanderi*, is a much smaller moss and has leaf tips that spread in many directions.

Fabronia pusilla Raddi [Fabroniaceae]
   Fabronia is divided into only three species, and so far only *Fabronia pusilla* has been collected in the Santa Monica Mountains. The tiny creeping silvery hair moss that forms thin mats in crevices and downwardly facing rock overhangs occurs principally in mediterranean climates and reaches its northern limit in southern British Columbia where it has been listed as endangered. Magnification of this very small moss will reveal broadly ovate leaves with long marginal teeth and elongate thin-walled cells. A species usually of seasonally dry habitats, *Fabronia pusilla* is elsewhere found also on tree bark, especially on oaks, but in the Santa Monica Mountains it appears to prefer rock. It occurs as small patches and often mingles with other bigger species which may outcompete it, contributing to its relatively low abundance.
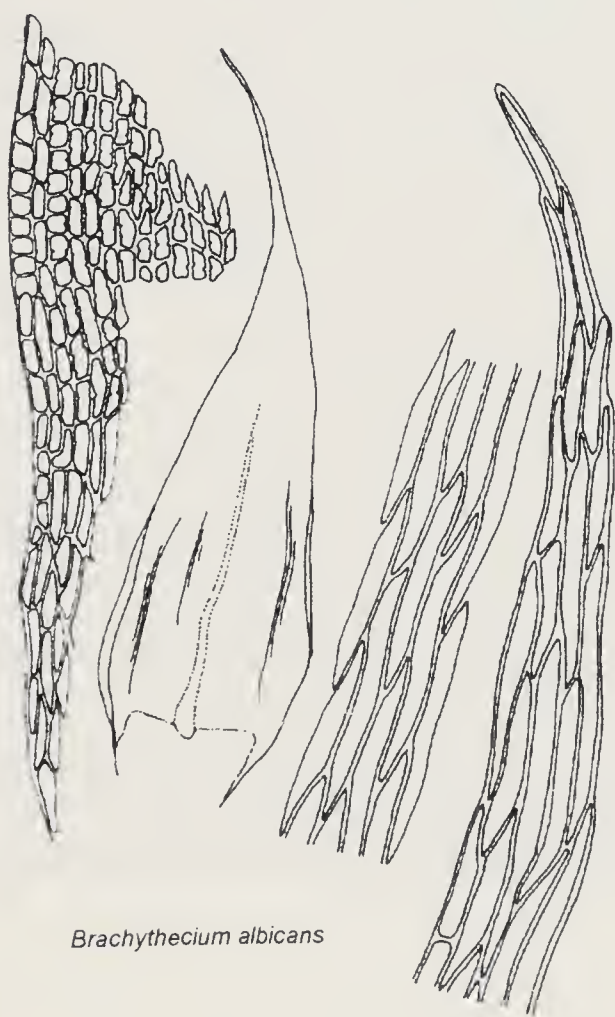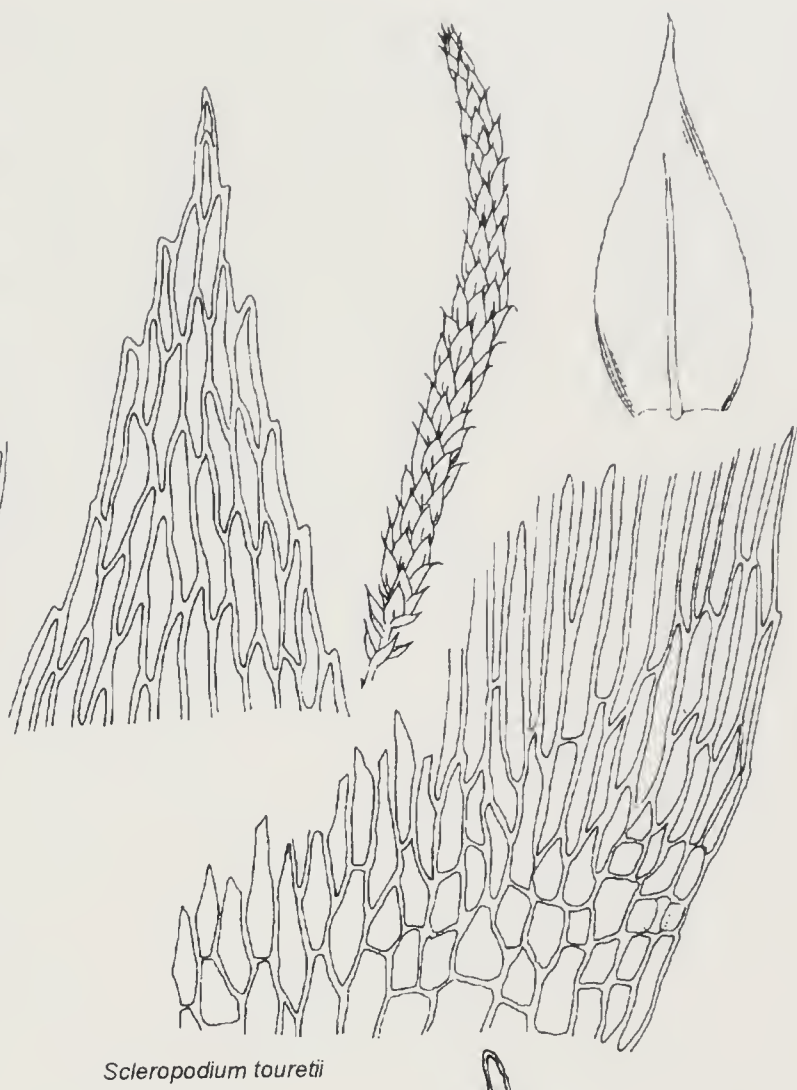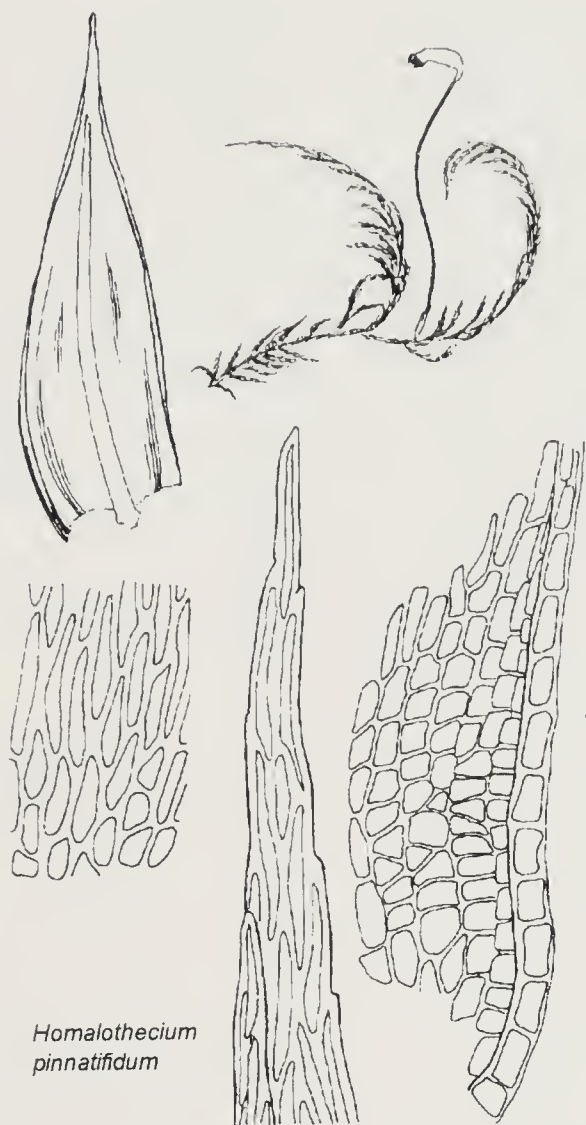
Homalothecium
pinnatifidum

Scleropodium touretii

Brachythecium albicans

Fabronia pusilla

Plate 11: Liverworts and a hornwort
(clockwise, from upper left):

Asterella californica (Hampe) Underw. [Aytoniaceae]
   Asterella ("little star" in reference to the starlike appearance of pores in the thallus of some species) form light green colonies on moist soil, and are found frequently in shaded locations in the drainages, along trail-cuts and sometimes under shrubs in coastal sage scrub in more shaded humid locations. The genus is widespread in many climates in both hemispheres, but reaches its greatest diversity in subtropical and milder temperate regions (Schofield 2002). *Asterella californica* is the most common thalloid liverwort in the Santa Monica Mountains, but it shows great variability in abundance between seasons and locations, and vegetative plants may be easily confused with other species of the genus or even with other genera such as *Targionia*. The sporophytes, however, are born on strongly 4- or 5-lobed carpocephala (umbrella-like heads) on stalks above the thallus.

Cryptomitrium tenerum (Hook.) Austin ex Underw. [Aytoniaceae]
   When reproductive, this monotypic genus is quickly recognized for the rather flat or shallowly domed spring-green carpocephalum. The plants have a thin, light green, flattened, dichotomously branching thallus that is sometimes somewhat shiny and purplish beneath. *Cryptomitrium* grows on soil and favors deep shade in very humid areas. Although not abundant in the Santa Monica Mountains, it is found occasionally in most deeper narrower drainages with some year round water.

Riccia trichocarpa M. Howe [Ricciaceae]
   Riccia are small, dichotomously branching thallose liverworts. The genus is the most species-rich of heptatic genera in California and is represented by four species in the Santa Monica Mountains. Typical to the species in this group, *Riccia* often grow mixed together or at least in the same general area on exposed rocky, summer-dry soil. Widespread in California, *Riccia trichocarpa* is perhaps the most distinctive of the local *Riccia* for its long hairs lining the thallus margins.

Phaeoceros carolinianus (Michx.) Prosk. [Notothyladaceae]
   Thallus morphology of *Phaeoceros* is extremely variable even within a species across the seasons and different habitats depending on the amount of moisture and exposure. *Phaeoceros carolinianus* has a dark, somewhat bluish-green thallus that may be flat or in wetter areas undulate. Except for the yellow spores, the distinguishing features of this species (the large angular chloroplasts with a visible central pyrenoid, lack of tubers, spores with a spinose distal face and rounded tuberculate proximal face) all require the use of a compound microscope. The only other hornwort genus confirmed for the Santa Monica Mountains, *Anthoceros*, has blackish spores, and unlike *Phaeoceros*, it has large mucilage- or air-filled cavities on the thallus whose margins tend to be crisped.

Porella bolanderi (Austin) Pearson [Porellaceae]
   Porella, a large nearly cosmopolitan but mainly east Asian genus, is the most common of the leafy liverworts found in the Santa Monica Mountains (the other being *Cephaloziella*). Elsewhere the plants may grow on soil or trees but in the Santa Monica Mountains they seem to prefer mostly vertical rock faces, forming often large patches. The species of *Porella* are often difficult to identify because of their plasticity which makes several of them nearly fade from one to the next.

Asterella californica

Cryptomitrium tenerum

Riccia trichocarpa

Targionia hypophylla

Fossombronia longiseta

Riella bolanderi

Targionia hypophylla L. [Targioniaceae]

The green to blue-green vegetative plants of *Targionia hypophylla* are reminiscent of narrow young *Asterella* plants, but tend to be more elongate and strongly incurved when dry. The reproductive plants, however, bear the unmistakable *Targionia* signature of a purplish black blister, the immersed sporophyte, under the tip of the thallus branch, which is usually present.

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DUDLEYA, WITH SPECIAL REFERENCE TO THOSE GROWING IN THE SANTA MONICA MOUNTAINS

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ABSTRACT: A brief overview of the taxonomic history and biogeography of *Dudleya* is given. Some of the more interesting aspects of the biology of *Dudleya* are recited, including physiological, foliar, and reproductive adaptations to the environment in which they are found. *Dudleya* taxa of the Santa Monica Mountains region are listed with brief descriptions of their appearance, habitat, range, and reproduction, and characteristics are compared between rare and more common taxa. Seedling survival and germination percentages do not differ significantly between rare and common taxa. The rare local taxa tend to have shorter inflorescences, fewer fruits, and fewer seeds per fruit than common local taxa do. Additionally, a majority of the individuals of the rare taxa reproduce in their first spring, while the common taxa had none or very few of their individuals reproduce in their first spring.

KEYWORDS: *Dudleya*, rarity, Santa Monica Mountains, succulent

INTRODUCTION

Dudleya is a genus of succulent plants in the family Crassulaceae that has evolved into many species, subspecies, and local races, mostly in southern California, Northern Baja California, and the California Islands. Presumably this has been quite recent, since many of them are restricted to geologically young terrain (Uhl 1994, 2004). In the Santa Monica Mountains region, nine *Dudleya* taxa are found. Three of them are common 'species' found in many habitats throughout the Santa Monicas and beyond. One is rare with intermediate habitat restrictions and range size. Five of them have much smaller ranges and seem to have restricted patterns of occurrence within the region (Bartel 1993; USFWS 1999). This review begins with a sketch of the taxonomic and geographic diversity that gives circumstantial evidence on their evolutionary radiation. Then it presents a treatment of the special features of these plants. It concludes with an accounting of the diversity of life histories and identifying characters of the rare and common species of *Dudleya* found in and around the Santa Monica Mountains.

TAXONOMY AND BIOGEOGRAPHY

It has been difficult for taxonomists to circumscribe taxa in the genus *Dudleya* because these plants look very similar to plants in other genera of Crassulaceae. In the past, *Dudleya* taxa have been variably classified under *Echeveria, Cotyledon, Sedum, Hasseanthus,* and *Styllaphyllum* (Thiede 2004; Moran 1953, 1942). This similarity in appearance is due partially to convergence (Uhl 2004; Walther 1936); plants of these genera grow under similar climatic conditions that have led to the parallel evolution of morphological characteristics adapted to those conditions (Uhl 2004). Within the genus it is difficult to define species and subspecies clearly because plants often occur in isolated populations with localized differentiation. Closely related taxa tend to intergrade with each other without clear-cut distinctions between the taxa (Thiede 2004). In 1803

Haworth named the first species that is now considered a *Dudleya*, as *Cotyledon caespitosa* (Thiede 2004). In 1828 DeCandolle named the genus *Echeveria* and included *C. caespitosa*. In 1903 Britton and Rose proposed *Dudleya, Stylophyllum,* and *Hasseanthus* as genera (Uhl 2004). New species were named under several genera until Moran revised the genus starting around 1940 (Moran 1942, 1953).

Thiede (2003) follows Bartel (1993) and Moran (1951) in separating *Dudleya* into three subgenera: *Dudleya* (31 species), *Stylophyllum* (9 species), and *Hasseanthus* (4 species), based on stem type, leaf structure, leaf shape, and corolla shape. Both subgenera *Dudleya* and *Stylophyllum* have aboveground branching stems with evergreen, perennial leaves, and they retain their old dried leaves. Subgenus *Hasseanthus* has unbranched subterranean stems and vernal soft leaves that die prior to flowering. Subgenus *Dudleya* usually has broad flattened leaves and erect tube-like corollas. Subgenus *Stylophyllum* usually has narrow leaves that are round to elliptic in cross-section and free petals erect from below but spreading from the middle (Thiede 2003). Subgenus *Hasseanthus* has narrowly linear, terate, or oblanceolate leaves that are sometimes slightly flattened (Abrams 1944) and widely spreading free petals (Thiede 2004). Although this breakdown into three subgenera is widely used, none of the subgenera is monophyletic (Burton 2002), so further work is required before the infragenetic taxonomy of *Dudleya* is put in good order.

Dudleya taxa are found mostly along the coast in Alta and Baja California, although one or two taxa reach into southwestern Oregon, and two get as far inland as Arizona. Subgenus *Dudleya* has the largest range, covering the entire region of the genus. Subgenus *Stylophyllum* is found in coastal or near-coastal areas, or islands from the Palos Verdes Peninsula south to Punta Baja, Baja California Norte. Subgenus *Hasseanthus* has a similar range as *Stylophyllum,* except that it is found farther to the north and not as far south in coastal and near-coastal areas (Thiede 2003, 2004; McCabe *in prep* 2008).

The coasts of Alta and Baja California have not always looked as they do now. This area has been shaped by the movement of two large plates: the Pacific Plate and the North American Plate. These plates meet along the coast of California above San Francisco Bay, and run south through California along its Coastal, Peninsular, and Transverse Ranges, and further south of California through the Gulf of California. Movement of the plates has pushed together a variety of rocks called terranes. These have differing histories; they originated at different times from various sources that were different distances from where they now occur. These terranes are found along the coastal mountains of California. Baja California once lay on the coast of Mexico but was pushed onto the Pacific Plate and moved northwest to its present location. *Dudleya* taxa are mostly found on the Pacific Plate, whereas *Echeveria* and other Mexican genera within the Crassulaceae family are found on the North American Plate. This suggests that *Dudleya* taxa were derived from ancestors in the northern mountains that migrated onto the coastal regions of the Pacific Plate, moving south and diversifying on the terranes, while *Echeveria* originated in Mexico and moved to the north (Uhl 2004, 1994). The closest relative to *Dudleya* is not known but is speculated to be *Sedum* in the section *Gormania* because they share the rosulate habit which is not found in other American members of the Leucosedum clade (Thiede 2004; Uhl 2004). Molecular data studies of the Crassulaceae place *Dudleya* in the Leucosedum clade whereas *Echeveria* is placed in the Acre clade (Thiede 2004; Mort et al. 2001). This distinction is corroborated by the fact that all *Dudleya* species have 17 pairs of chromosomes or multiples thereof whereas *Echeveria* species vary greatly in chromosome number. Also, *Dudleya* species do not hybridize with other Crassulaceae while *Echeveria* species do (Uhl 2004, 1994).

PHYSIOLOGY & MORPHOLOGY

There are different metabolic pathways by which a plant may carry out photosynthesis. One such pathway is Crassulacean Acid Metabolism (CAM). CAM photosynthesis differs from other photosynthetic pathways in that CAM plants open their stomata at night, whereas C_3 plants open their stomata during the day. When a plant's stomata are open it allows the intake of CO_2 from the air, release of O_2, and the loss of water vapor from the plant. CAM plants tend to grow in arid environments, where it is adaptive to minimize water loss by opening the stomata when temperatures are cooler and relative humidity is higher (Hall & Rao 1999). While it is advantageous for plants to use the CAM pathway under dry conditions, the C_3 pathway fixes more carbon under wet conditions (Throughton et al. 1977), allowing for more rapid growth.

Seven *Dudleya* taxa have been shown to have the ability to facultatively change which photosynthetic pathway they use based on the amount of available moisture (Bartholomew 1973; Throughton et al. 1977; Teeri 1984). This ability is of particular importance to *Dudleya* because they grow in a mediterranean climate with wet mild winters and dry hot summers (Bartholomew 1973). During the wet season, when the plants are growing, most of the CO_2 uptake is during the day (C_3 pathway). At the end of spring and into summer, as the soil becomes dry, the plants shift to CO_2 uptake at night (CAM pathway). The ability of the plants to conserve water when conducting photosynthesis allows them to survive the summer drought (Teeri 1984; Throughton et al. 1977; Bartholomew 1973). Ting and Rayder (1982) tested the reaction of CAM plants to water stress. Some plants changed to a photosynthetic pathway Ting and Rayder termed "CAM-idling." Plants that are "CAM-idling" keep their stomata closed all the time, night and day, and they photosynthesize only at a low level. These plants have no net CO_2 uptake and therefore do not grow, but they are able to sustain themselves in this state without losing water through open stomata. *Dudleya* plants become dormant during the summer drought and may well be able to survive by switching to "CAM-idling."

One adaptation that varies by environment is the amount of wax on the leaves. In *D. brittonii* D. A. Johansen, some plants have leaves that are glaucous (with epicuticular wax) and others have leaves that are non-glaucous (without wax). Plants growing in more exposed habitats have glaucous leaves, while plants growing in shaded habitats and better-developed soil generally have non-glaucous leaves. Plants with glaucous leaves are thought to have several advantages over non-glaucous plants, including protection from: ultraviolet radiation, fungal pathogens, frost damage, herbivory, nutrient loss from leaching in foggy areas, leaf loss during drought, and breakdown of proteins, nucleic acids, and chlorophylls in stressed leaves. The disadvantage of having glaucous leaves is presumably that the plant is less competitive, especially at low light levels (Mulroy 1979). *Dudleya* taxa vary in how glaucous their leaves are, so these adaptations are likely not limited to *D. brittonii* alone (Manheim et al. 1979). For example, the very glaucous foliage of *D. pulverulenta* subsp. *pulverulenta* may explain its relative tolerance to sun.

Other adaptations relate to reproduction. There are two main groups of pollinators for *Dudleya* taxa depending on corolla size, color, and degree of petal fusion (Aigner 2004). Taxa with small yellow to orange flowers are pollinated by bees and flies small enough to enter the corolla and other insects too big to enter the flower but with tongues long enough to reach the nectar. Other taxa, with big red flowers, are pollinated by hummingbirds (Levin & Mulroy 1985). Flowers with widely spreading petals or that are fused at the base but open at the tip attract bees and flies, while those that have fused tube-like corollas tend to be hummingbird pollinated (Aigner 2004). Sugar content and concentration in nectar, and volume produced differ by pollinator. Hummingbird-pollinated flowers have a higher energy content and produce more nectar than bee- and fly-pollinated flowers. Further, the amount of nectar produced is related to the degree of auto-fertility

(ability of the plant to fertilize itself) of the taxa. Taxa with high nectar production have lower auto-fertility (<20%) than taxa with low nectar production (25 - 50%). Taxa with higher auto-fertility are likely to experience pollinator unreliability, short and unpredictable reproductive seasons, high population turnover, and small population size. Auto-fertility increases the likelihood of reproductive output. If cross-fertilization does not occur, the plant can still reproduce via self-fertilization (Levin & Mulroy 1985). In general, *Dudleya* seeds sprout in the winter once the rains have begun. Plants grow over the rainy season and produce inflorescences in spring. Plants flower for two to three months. Over the summer outer leaves, inflorescences, and fruits dry and the plant goes dormant. Fruits consist of five follicles that split open to release the seeds in late summer and fall (pers. obs.). Perhaps the most intriguing diversity among *Dudleya* taxa is in features that seem to relate to life history, for example having underground storage organs by which a plant over-summers and reproducing even in the first year after germination as opposed to delaying reproduction and having a large rosette aboveground. This life-history diversity is well represented among the taxa found in and around the Santa Monica Mountains.

DUDLEYA DIVERSITY IN THE SANTA MONICA MOUNTAINS REGION

Dudleya taxa typically inhabit ocean bluffs, sheer cliffs, and rock outcrops including open habitat soils that have nutrient-poor substrates and little vegetation (Riefner et al. 2003). Local taxa tend to be found in coastal, subcoastal, or both coastal and interior sites. Taxa that are coastal occur within a mile or so of the coast or also on islands. Taxa that are subcoastal are found within 1 and 15 miles of the coast. Coastal and interior taxa are found both on or near the coast and inland 30 miles or more (Moran 1951). Taxa growing inland tend to be in sites that are north facing or deeply shaded (Riefner et al. 2003). The Santa Monica Mountains harbor these diverse habitat types and are the home of five rare narrowly endemic species (see Figure 1 for locations of rare *Dudleya* taxa in the Santa Monica Mountains region). These rare *Dudleya* taxa are often found growing with mosses, lichens, and *Selaginella*. Lichens and mosses may act as nurseries and provide a substrate, moisture, and nutrients for *Dudleya* seed recruitment as well as protection against snail and slug herbivory (Riefner & Bowler 1995, Riefner et al. 2003). Following is an account of *Dudleya* taxa found in the Santa Monica Mountains region with descriptions of the plant, habitat type, range, and reproduction. Table 1 then presents a summary of the field observations for each of the nine *Dudleya* taxa found in the Santa Monica Mountains region, while Table 2 presents observations on germination, survivorship, morphology, and flowering of cultivated seedlings during the first six months of life for each of those taxa. Figures 2 and 3 present photographs of those nursery-grown plants.

D. parva Rose & Davidson (*D. abramsii* subsp. *parva* per Bartel 1993)   CONEJO LIVE-FOREVER

Status: federally listed as threatened.
Description: This taxon differs from other locally threatened taxa in that it forms a rosette of oblanceolate leaves that are vernal, completely drying during the summer drought. Flowers are a pale yellow and may be flecked with red on the keel (USFWS 1999).
Habitat and Range: This subcoastal taxon (Moran 1951) grows in Conejo volcanic soils, which tend to be shallow and rocky, in coastal sage and grassland habitats within a discontinuous 10-mile range in Ventura County, north of the Ventura Freeway (US 101) (USFWS 1999).
Inflorescence height: 13 cm (high end of low range)
Number of fruits produced: 24 (low end of range)
Maximum # of seeds per fruit: 79 (second lowest)
% with inflorescence: 100%

Santa Monica Mountains Dudleya

- *D. blochmaniae spp. blochmaniae*
- *D. cymosa spp. agourensis*
- *D. cymosa spp marcescens*
- *D. cymosa spp ovatifolia*
- *D. parva*
- *D. verityi*
- major roads
- Santa Monica Mountains
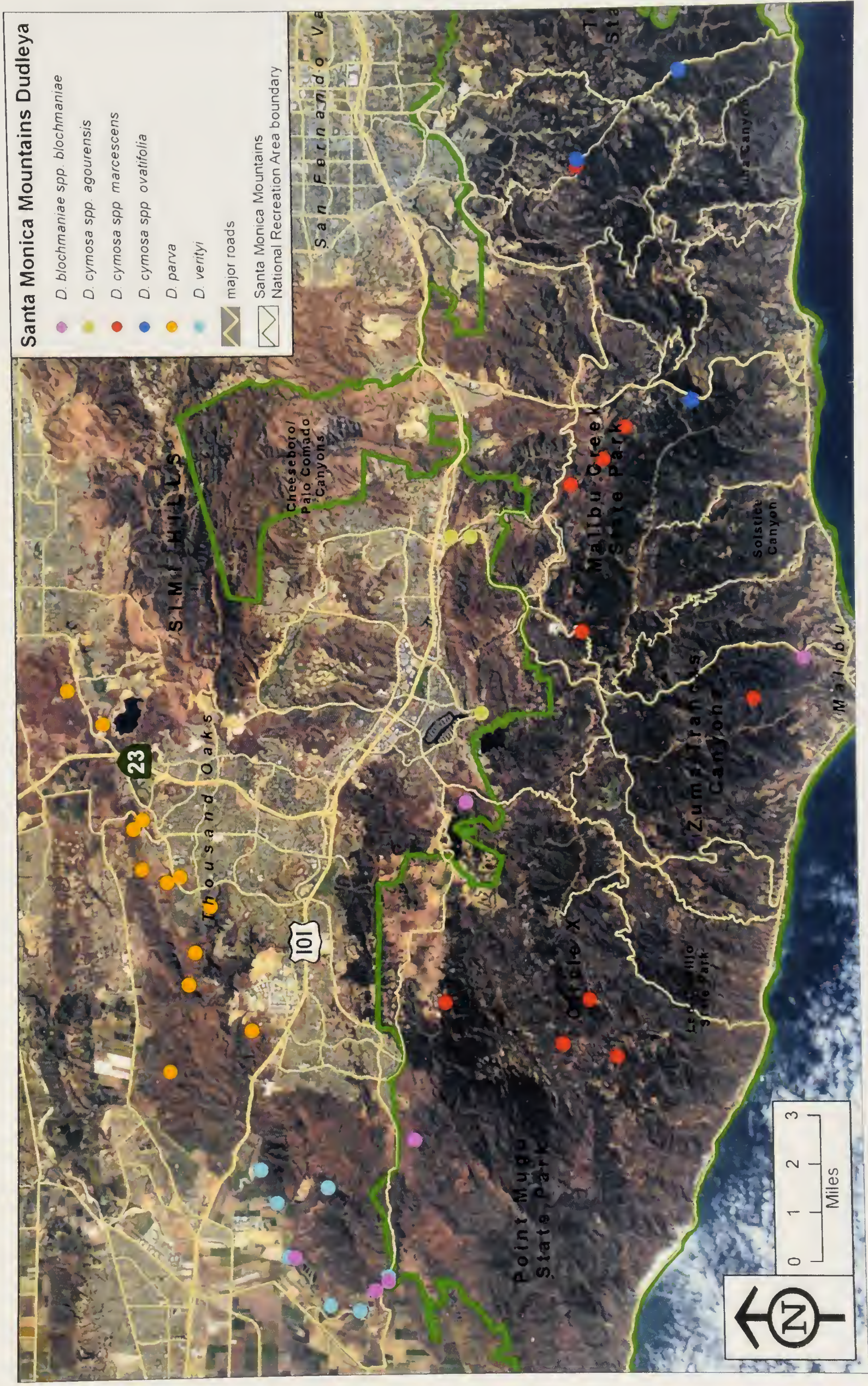- National Recreation Area boundary

Figure 1. Map of rare *Dudleya* taxa mapped in the Santa Monica Mountains Region. Map produced by Tarja Sagar and Lena Lee.

D. blochmaniae (Eastw.) Moran subsp. *blochmaniae*   BLOCHMAN'S DUDLEYA

Status: rare.

Description: Unlike the rest of the local *Dudleya* taxa, this taxon belongs to the subgenus *Hasseanthus* (Thiede 2004). Their rosettes are of yellow-green, linear-oblanceolate to linear-spatulate, vernal leaves, all withering completely by summer. Corollas are white with violet or red markings, commonly with a rose-colored dorsal mid-stripe (Thiede 2003).

Habitat and Range: This coastal taxon (Moran 1951) occurs on open rocky slopes, often clay or serpentine, from the central south and south coast of California to northern Baja California (Bartel 1993; Thiede 2003; Safford et al. 2005).

Additional information: These plants are corm-forming and survive the summer drought by dying back to the corm only, from which new leaves sprout in the winter. The corms have the ability to stay hydrated over long periods of time, even when soil moisture is immeasurably low (Teeri 1984).

Inflorescence height: 11 cm (lowest of range)

Number of fruits produced: 29 (low end of range)

Maximum # of seeds per fruit: 36 (the lowest)

% with inflorescence: 98%

D. veretyi K. Nakai   VERITY'S DUDLEYA

Status: federally listed as threatened.

Description: These plants form clusters of rosettes, 25-100 or more, from 10-40 cm wide. Leaves are oblong-lanceolate and glaucous. The corollas are lemon yellow with slightly green midribs near the tip of the petals (Nakai 1983).

Habitat and Range: They grow in a coastal sage scrub habitat on volcanic rock found along a discontinuous 4-mile range in Ventura County south of the Ventura Freeway (USFWS 1999).

Inflorescence height: 12 cm (low end of range)

Number of fruits produced: 39 (high end of low end of range)

Maximum # of seeds per fruit: 112 (mid-range)

% with inflorescence: 95%

D. cymosa (Lemaire) Britton & Rose subsp. *marcescens* Moran   MARCESCENT DUDLEYA

Status: federally listed as threatened and state listed as rare.

Description: This taxon differs from other local taxa in that it has marcescent leaves, drying during the summer but remaining attached to the plant (USFWS 1999). These plants have green oblanceolate leaves and bright yellow petals often marked with red (Moran 1957).

Habitat and Range: This subcoastal taxon (Moran 1951) usually occurs on canyon walls close to perennial streams or sheer volcanic rock in the lower reaches of those streams within a 15-mile range in Los Angeles and Ventura Counties, south of the Ventura Freeway (USFWS 1999).

Inflorescence height: 11 cm (lowest of range)

Number of fruits produced: 10 (lowest of range)

Maximum # of seeds per fruit: 144 (mid-range)

% with inflorescence: 76%

Discussion: Levin & Mulroy (1985) found that mechanical cross-pollination increased seed set compared to self-pollination (15 *Dudleya* taxa), in some cases by two or more times. Furthermore, pollination services to *D. cymosa* subsp. *marcescens* may be less than for other *Dudleya* taxa because they grow in microhabitats with no other flowering plants (USFWS 1999).

Seed set for these individuals ranged from 12–144 (unpublished data). The high seed set values may reflect cross-pollinated flowers, while the lower seed set values reflect self-pollinated flowers. In addition, seedling survival at seven weeks was less for seeds that had been self-pollinated than for cross-pollinated ones in five of six *Dudleya* taxa (Levin & Mulroy 1985). The low percentage of seedling survival could be because the seeds came from self-pollinated flowers. This is especially likely for plants from one of the populations in Los Angeles County, as it had few flowering plants and therefore, probably would not attract many pollinators (pers. observ.).

D. cymosa subsp. *agourensis* K. Nakai   AGOURA LIVE-FOREVER

Status: federally listed as threatened.
Description: This taxon grows a rosette of elliptic to oblong glaucous leaves and has bright yellow petals that are occasionally glaucous along the midrib (Nakai 1987).
Habitat and Range: This subcoastal taxon (Moran 1951) grows on exposed west- to northwest-facing volcanic rock outcrops (Nakai 1987) found south of the Ventura Freeway in Los Angeles County (USFWS 1999).
Taxonomic note: Thiede (2003) and Bartel (1993) include *D. cymosa* subsp. *agourensis* in *D. cymosa* subsp. *ovatifolia*. *D. cymosa* subsp. *agourensis* differs from *D. cymosa* subsp. *ovatifolia* morphologically in basal leaf shape and color, caudex branching, pedicel size, and degree of petal spreading. The two subspecies also differ in the habitats in which they are found (Nakai 1987). Furthermore, subspecies *agourensis* has longer leaves and taller inflorescences, twice as many leaves (Table 1) and greater seedling survival, 92% vs. 81% than subspecies *ovatifolia* (Table 2).
Inflorescence height: 26 cm (low end of mid-range)
Number of fruits produced: 74 (mid-range)
Maximum # of seeds per fruit: 122 (mid-range)
% with inflorescence: 57%

D. cymosa subsp. *ovatifolia* (Britton) Moran   SANTA MONICA MOUNTAINS DUDLEYA

Status: federally listed as threatened.
Description: These plants have a unique appearance in that they form a rosette of ovate to elliptic, evergreen, non-glaucous leaves (Moran 1951) with maroon undersides (Nakai 1983). The corollas are bright yellow (Moran 1951).
Habitat and Range: This subcoastal taxon (Moran 1951) tends to grow on sedimentary conglomerate rock on canyon bottoms and shaded slopes found south of the Ventura Freeway in Los Angeles County and in the Santa Ana Mountains (USFWS 1999; Nakai 1987).
Inflorescence height: 11 cm (lowest of range)
Number of fruits produced: 19 (low end of range)
Maximum # of seeds per fruit: i14 (mid-range)
% with inflorescence: 53%

D. lanceolata (Nutt.) Britton & Rose   LANCE-LEAF LIVE-FOREVER

Status: common.
Description: Forms rosettes of glaucous or green oblong-lanceolate leaves (Moran 1951). Flowers can be yellow, mostly red, red-tinged, or patterned outside and orange-yellow to greenish inside (Thiede 2003).

Habitat and Range: This taxon grows widely in both coastal and interior sites (Moran 1951) on rocky slopes of chaparral and coastal sage scrub habitats in California's South Coast, Transverse, and Peninsular Ranges and desert mountains as well as in northern Baja California (Thiede 2003; McAuley 1996; Bartel 1993).

Taxonomic note: see *D. caespitosa*

Inflorescence height: 69 cm (high end of range)

Number of fruits produced: 83 (mid-range)

Maximum # of seeds per fruit: 274 (second highest)

% with inflorescence: 10%

D. caespitosa (Haw.) Britton & Rose   LIVE-FOREVER

Status: common.

Description: This taxon grows rosettes sometimes as large as 60 cm in diameter with clumps of more than 150 rosettes. Leaves can be glaucous or non-glaucous, mostly oblong to oblong-oblanceolate. Corollas are generally bright yellow to red (Moran 1951).

Habitat and Range: This subcoastal taxon (Moran 1951) occurs on sandy bluffs and rocks, generally within 100 m of the coast from the north-central and central coast of California to the northern Channel Islands (Bartel 1993; McAuley 1996; Thiede 2003; McCabe *in prep* 2008).

Taxonomic note: This species has been reported from the Santa Monica Mountains (McAuley 1996), but plants so identified may turn out to be more closely related to *D. lanceolata* (S. McCabe pers. comm.). *D. caespitosa* intergrades seemingly continuously with *D. lanceolata* and three other *Dudleya* species (Moran 1951).

Inflorescence height: 49 cm (mid-range)

Number of fruits produced: 88 (mid-range)

Maximum # of seeds per fruit: 196 (third highest)

% with inflorescence: 0%

D. pulverulenta (Nutt) Britton & Rose subsp. *pulverulenta*   CHALK LIVE-FOREVER

Status: common.

Description: Has large rosettes, up to 20" in diameter (McAuley 1996) and is covered with a characteristic white mealy powder to dense wax (Bartel 1993). Leaves are oblong to obovate (Moran 1951). The corolla is deep red with pink stripes (McAuley 1996). Flowers tend to be pendent in bud and erect in fruit (Moran 1951).

Habitat and Range: This taxon occurs in both coastal and interior sites (Moran 1951) on rocky cliffs, canyons, and slopes in coastal sage scrub and chaparral habitats from south-central and southern California to northern Baja California (Bartel 1993; McAuley 1996; Thiede 2003; McCabe *in prep* 2008). Unlike other local taxa, this taxon is more tolerant to sun in that it occurs on non- north facing, non-shaded slopes (pers. obs.).

Inflorescence height: 88 cm (highest)

Number of fruits produced: 167 (highest)

Maximum # of seeds per fruit: >1000 (highest)

% with inflorescence: 0%

Discussion: This taxon is hummingbird pollinated, which is an unreliable form of pollination for *Dudleya* (Levin & Mulroy 1985), since many of the seeds are likely the result of self-pollination. This could explain its poor seedling survival percentages (see *D. cymosa* subsp. *marcescens* and Table 2).

Table 1. Field observations of nine *Dudleya* taxa.

	Longest leaf length	# Leaves	Inflorescence height	# Fruits	Maximum # of seeds per fruit	Nearest neighbor distance	Slope	Aspect	Shade	Flowering season
*Dudleya parva**	N/A	N/A	13 cm	24	79	10.8 cm	0-90° most 10°	20-0-300° most w/in 10° of N	Only by rock outcrops	May - June
Dudleya blochmaniae subsp. *blochmaniae**	N/A	N/A	11 cm	29	36	7.4 cm	0-40° most 20°	30-0-310°	Only by rock outcrops	May - June
*Dudleya verityi**	1.6 cm	8	12 cm	39	112	6.3 cm	10-90°	55° - 0° - 270o	Only by rock outcrops	May - June
Dudleya cymosa subsp. *marcescens**	1.4 cm	5	11 cm	10	144	6.6 cm	55-90°	30° & 350°	By trees	May - June
Dudleya cymosa subsp. *agourensis**	2.6 cm	10	26 cm	74	122	68.3 cm	25-90°	90-0-340°	Only by rock outcrops	May - June
Dudleya cymosa subsp. *ovatifolia**	1.8 cm	5	11 cm	19	114	25.8 cm	10-90° most >50°	0-180°	By trees or far side of canyon	March - May
Dudleya lanceolata	3.8 cm	7	69 cm	83	274	168 cm	0-90°	50-0-140°	Variable	May – July
Dudleya caespitosa	6.4 cm	16	49 cm	88	196	50.8 cm	0-90° most 90°	230-0-320°	Only by rock outcrops	April - May
Dudleya pulverulenta subsp. *pulverulenta*	11.7 cm	44	88 cm	167	>1000	501.4 cm	0-90° 1/3 at 90°	20-0-340°	Variable	May – July

Asterisk indicates rare taxon. Data were collected from sites in the Santa Monica Mountains Region over the summer of 2005. Plants were chosen from two or three populations for each taxon. *D. parva* and *D. blochmaniae* subsp. *blochmaniae* did not have leaves at the time of data collection. Longest leaf length, averaged (n = 30), Number of leaves. averaged (n = 30), Inflorescence height, height of the tallest inflorescence per plant, averaged (n = 30), Number of fruits per plant, averaged (n = 30), Nearest neighbor distance. distance of the five nearest neighbors to the focal plant of the same species, averaged (n = 30). Slope of substrate plant was growing on, averaged (n = 30). Range of aspects for plants (n = 30). Flowering season for plants growing in the Santa Monica Mountains from McAuley (1996).

Table 2. Observations of cultivated seedlings during the first six months of life.

	% germinated	% survived to transplantation	Longest leaf length	# Leaves	% with inflorescence
*Dudleya parva**	77%	94%	5.9 cm	7	100%
Dudleya blochmaniae subsp. *blochmaniae**	74%	87%	2.7 cm	3	98%
*Dudleya verityi**	60%	87%	6.9 cm	20	95%
Dudleya cymosa subsp. *marcescens**	43%	86%	4.2 cm	14	76%
Dudleya cymosa subsp. *agourensis**	64%	92%	5.6 cm	18	57%
Dudleya cymosa subsp. *ovatifolia**	59%	81%	4.8 cm	13	53%
Dudleya lanceolata	80%	96%	8.4 cm	15	10%
Dudleya caespitosa	73%	94%	9.2 cm	18	0%
Dudleya pulverulenta subsp. *pulverulenta*	63%	81%	4.8 cm	16	0%

Asterisk indicates rare taxon. Seeds collected from two or three populations of each taxon in the Santa Monica Mountains Region the summer of 2005. Seeds were sown in December 2005 in 4" pots, 30 seeds per pot in a greenhouse and were fertilized weekly. Seedlings were transplanted between the ages of two to four months, one individual per 4" pot and placed in a shade house. Percentage germinated = maximum number of live seedlings per taxon divided by number of seeds sown. Percentage survived to transplantation = number of seedlings that survived to be transplanted divided by maximum number of seedlings. Longest leaf length and leaf number – leaf length and number at age six months were averaged for two plants from each seed parent then averaged for each taxon, except for *D. blochmaniae* subsp. *blochmaniae* (because so few plants had leaves, leaves per group were averaged, then averaged per taxon). Percent with inflorescence = plants with inflorescences during the first six months in each taxon for all experimental groups were totaled and divided by total number of plants per taxon in all groups.

D. parva

D. blochmaniae subsp. blochmaniae

D. verityi

D. cymosa subsp. agorensis

D. cymosa subsp. marcescens

Figure 2. *Dudleya* plants grown from seed collected in the wild in the Santa Monica Mountains Region at age 4-6 months.

Figure 3. *Dudleya* plants grown from seed collected in the wild in the Santa Monica Mountains Region at age 4-6 months.

CONCLUSIONS

Germination percentages and seedling survival (Table 2) did not differ substantially for rare and common taxa except in the case of *D. cymosa* subsp. *marcescens*, which will be discussed later. The rare local taxa tend to have shorter inflorescences, fewer fruits, and fewer seeds per fruit (Table 1) than common local taxa do. Also, the rare taxa had a majority of their individuals reproduce in their first spring (in Table 2 - those with an inflorescence) while the common taxa had very few or none of their individuals reproduce in their first spring. The rare and common taxa appear to have different reproductive strategies. The rare taxa tend to reproduce early and have subsequently lower reproductive output. The common taxa tend to reproduce later and have a subsequently greater reproductive output.

At one end of the spectrum are *D. parva* and *D. blochmaniae* subsp. *blochmaniae* (federally threatened and rare, respectively). They had a very high percentage of individuals (100% and 98 %, respectively) reproduce in their first spring (Table 2) and have reproductive outputs (Table 1) that are among the lowest of all taxa studied. These plants differ from the other local taxa in that their leaves are present only in the spring. Plants die back completely over the summer dry season and re-sprout in the winter from underground structures. The lack of evergreen leaves may result in less energy production for reproductive structures, but their underground storage organs may ensure reproduction every yearIn the middle of the spectrum is *D. cymosa* subsp. *marcescens* (federally threatened/ state rare). Although 76% of the seedlings reproduced in their first spring and seedling survival was 86% (Table 2), reproductive output is among the lowest of the local taxa (Table 1) and the percentage of seeds that germinated was only 43% compared to 59% or greater in all other local taxa (Table 2). The combination of low reproductive output and low seed germination puts this taxon in greater danger of extinction than the other rare local taxa. This is especially true because population persistence in *Dudleya* is dependant on seed production (Moran 1951). In addition, the lack of pollination services experienced by these plants can decrease seed set and seedling survival (Levin & Mulroy 1985).

At the other extreme is the common taxon, *D. pulverulenta* subsp. *pulverulenta*. It has the tallest inflorescence and the greatest reproductive output (Table 1), but did not have any individuals reproduce in their first spring (Table 2). These plants are larger than the other local taxa and may have a longer life span than they do. This means that germination and seedling survival percentages may not be as critical as for shorter-lived taxa; therefore, there may be less pressure to reproduce at an early age. Although all *Dudleya* seed is small, seeds of this taxon are notably smaller than those of the other local taxa (pers. obs.). Small seed size in combination with lessened pressure for seeds to germinate allows for seed production that far exceeds any of the other local taxa.

Since seed germination and seedling survival are close to the same for both rare and common local taxa (Table 2) it does not seem to be as important to population growth and persistence as reproductive output does. Furthermore, delay in reproduction leads to a greater likelihood of young plant survival and attainment of greater size before reproducing, which increases energy production and makes more energy available for reproductive structures. Common taxa tend to have taller inflorescences than rare taxa do (Table 1), which can lead to superior seed dispersal (Lloyd et al. 2003). Greater seed dispersal can lead to establishing populations in new areas, resulting in range expansion.

ACKNOWLEDGEMENTS

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MANAGING RARE PLANTS AT THE WILDLAND URBAN INTERFACE: AN EXAMPLE FROM THE SANTA MONICA MOUNTAINS AND SIMI HILLS

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ABSTRACT: When areas of high biological diversity lie in the path of expanding human populations, rare species often decline and become threatened or endangered with extinction. Conservation of plants at the wildland-urban interface presents many challenges including impacts of direct habitat loss and a multitude of direct and indirect impacts of habitat fragmentation. Here I use the example of managing rare and endangered plants in the Santa Monica Mountains and Simi Hills of California to review the difficulties and potential impacts of the wildland-urban interface on species conservation. *Pentachaeta lyonii*, a state and federally endangered plant in the Santa Monica Mountains, has lost 17% of its known occurrences to development within eight years. All occurrences of this species on public property have been invaded by non-native species known to negatively impact its growth and reproduction. The impacts of urbanization on pollination and seed dispersal of endangered plants in the Santa Monica Mountains and Simi Hills are as yet unknown but have the potential to cause population loss and even extinction over the long-term. Management challenges stemming from the complex matrix of public and private lands across the landscape have resulted in inconsistent population monitoring, insufficient habitat management, and population loss. Yet, the large populations in the region provide substantial opportunities for education, volunteerism, academic involvement, pooled agency resources, and partnerships with private landowners.

KEYWORDS: wildland-urban interface, rare plant conservation, fragmentation, habitat loss, genetic diversity, pollination, seed dispersal

INTRODUCTION

Many of the world's threatened and endangered species are found in close proximity to human population centers. When areas of high biological diversity and naturally rare species lie in the path of expanding human populations, rare species often decline and can become threatened or endangered with extinction. A recent analysis by Schwartz et al. found that 22 percent of endangered plants in the United States are found in the 40 largest metropolitan areas, which encompass only 8.4 percent of the land area (Schwartz et al. 2002). Models of protecting biodiversity by creating large nature reserves in biologically diverse areas may not present an accurate picture of species conservation in the United States or the world for much longer. As urban expansion begins to encroach on state and national parks, and as new areas are purchased for protection within urban matrices, a new reality of small protected areas in an urban or suburban matrix is emerging. I use the Santa Monica Mountains National Recreation Area, the United States' largest urban park, to discuss some of the unique challenges and opportunities presented by the wildland-urban interface in rare plant conservation and management.

BACKGROUND

The Santa Monica Mountains National Recreation Area (SMMNRA or Recreation Area) occupies 150,000 acres located near the greater Los Angeles, California area and is a mosaic of federal, state and private lands. The Recreation Area was created by Congress in 1978 to achieve several goals, including a) protecting an important remnant of the California Mediterranean Ecosystem b) protecting air quality for area residents and c) providing recreational and educational opportunities for the people of the Los Angeles basin and surrounding areas. Within the recreation area, land ownership is divided between private (85,000 acres), state (43,000 acres) and federal (22,000 acres). Public land ownership in the SMMNRA contains both large parcels (over 1,000 acres) and small parcels (1,000 acres or less). In addition to the recreation area itself, the Santa Monica Mountains Ecological Zone (SMMEZ) extends northward into the Simi Hills and contains an additional 75,000 acres. The issues discussed here apply to both the SMMNRA and the SMMEZ. Many of the endangered plant species in the region occur throughout the SMMEZ. Where possible, I give statistics on land use for both the SMMNRA and the SMMEZ.

The Natural Environment

The recreation area is floristically diverse with approximately 1,200 plant species documented in an ongoing review of the flora (see Prigge and Gibson, this volume), of which approximately 900 are native and 300 are non-native. Vegetation types within the SMMNRA include chaparral, coastal sage scrub, oak woodland, riparian, non-native grassland, native grassland, coastal strand, and wetlands (see Tiszler and Rundel, Keeler-Wolf et al., this volume). The recreation area is part of the California Floristic Province, which is well known for its high species richness and high rates of endemism (Stein et al. 2000). Due to the combination of high diversity and high rates of habitat loss, the California Mediterranean Ecosystem is noted as a global biodiversity hotspot (Myers et al. 2000).

Within the SMMNRA twelve plant taxa are listed either federally or at the state level as rare, threatened, or endangered (Table 1). Forty-one additional species are considered sensitive by the California Native Plant Society.

The Human Environment

The SMMNRA is a largely undeveloped area that extends into one of the United States' largest urban areas (Figure 1). Within the SMMNRA are two counties (Ventura and Los Angeles), seven incorporated cities (Thousand Oaks, Westlake Village, Agoura Hills, Calabasas, Malibu, Santa Monica, and Los Angeles), 265 homeowner associations, and 67 different cooperating government agencies. The population of the Los Angeles metropolitan region is currently 16.7 million and is expected to double within 40 years (Fulton 2001). Real estate within the region is expensive, with median home prices of approximately $560,000 (Forbes 2006). Therefore, purchasing land for conservation can be an expensive proposition.

Although a large proportion of open space remains undeveloped within the SMMNRA, 12.7 percent is already developed and over half of the total area is private land and thus available for some level of development (Figure 2). Within the SMMEZ, 21 percent of the land is currently developed. Ownership of public lands is divided between numerous local, state, federal, and non-profit land conservancies (Figure 3). Future development within the SMMNRA is likely to occur throughout the recreation area based on filed development permits (Figure 4) and urban growth models (Syphard et al. 2007). These land use patterns have resulted in an interdigitated patchwork of developed and undeveloped areas, fragmenting the remaining open space (Figure 5).

Table 1. State and Federally Listed Plant Taxa in the Santa Monica Mountains and Simi Hills. E = endangered, T = threatened, R = rare.

Species	State	Federal	Dispersal Mode
Astragalus brauntonii	--	E	Seed pods have sticky hairs and may be animal dispersed. Seed pods eventually dehisce and individual seeds are dispersed by wind or water.
Chorizanthe parryi ssp. *fernandina*	E	--	Unknown. No obvious seed dispersal adaptations.
Cordylanthus maritimus ssp. *maritimus*	E	E	Unknown. No obvious seed dispersal adaptations.
Dudleya abramsii ssp. *parva*	--	T	Unknown. Seeds are small and may be dispersed by wind, water or soil movement. No obvious seed dispersal adaptations.
Dudleya cymosa ssp. *agourensis*	--	T	Unknown. Seeds are small and may be dispersed by wind, water or soil movement. No obvious seed dispersal adaptations.
Dudleya cymosa ssp. *marcescens*	R	T	Unknown. Seeds are small and may be dispersed by wind, water or soil movement. No obvious seed dispersal adaptations.
Dudleya cymosa ssp. *ovatifolia*	--	T	Unknown. Seeds are small and may be dispersed by wind, water or soil movement. No obvious seed dispersal adaptations.
Dudleya verityi	--	T	Unknown. Seeds are small and may be dispersed by wind, water or soil movement. No obvious seed dispersal adaptations.
Eriogonum crocatum	R	--	Seeds are small and light. Wind dispersal is most likely mechanism.
Hemizonia minthornii	R	--	Seeds have short bristles. Dispersal in animal fur is likely. Wind dispersal also likely.
Orcuttia californica	E	E	Small grass seeds. Most likely wind and water dispersed.
Pentachaeta lyonii	E	E	Seeds are small and light with potential for wind, water, or animal dispersal.

Figure 1. *Regional Context of the Santa Monica Mountains National Recreation Area.* The SMMNRA occurs in a region with both large urban areas (Los Angeles) and large areas of open space (Los Padres and Angeles National Forests).

Figure 2. *Land Use Within the Santa Monica Mountains National Recreation Area.* The SMMNRA contains both undeveloped and developed lands. Over 50% of the undeveloped land is privately owned and is thus available for development in the future.
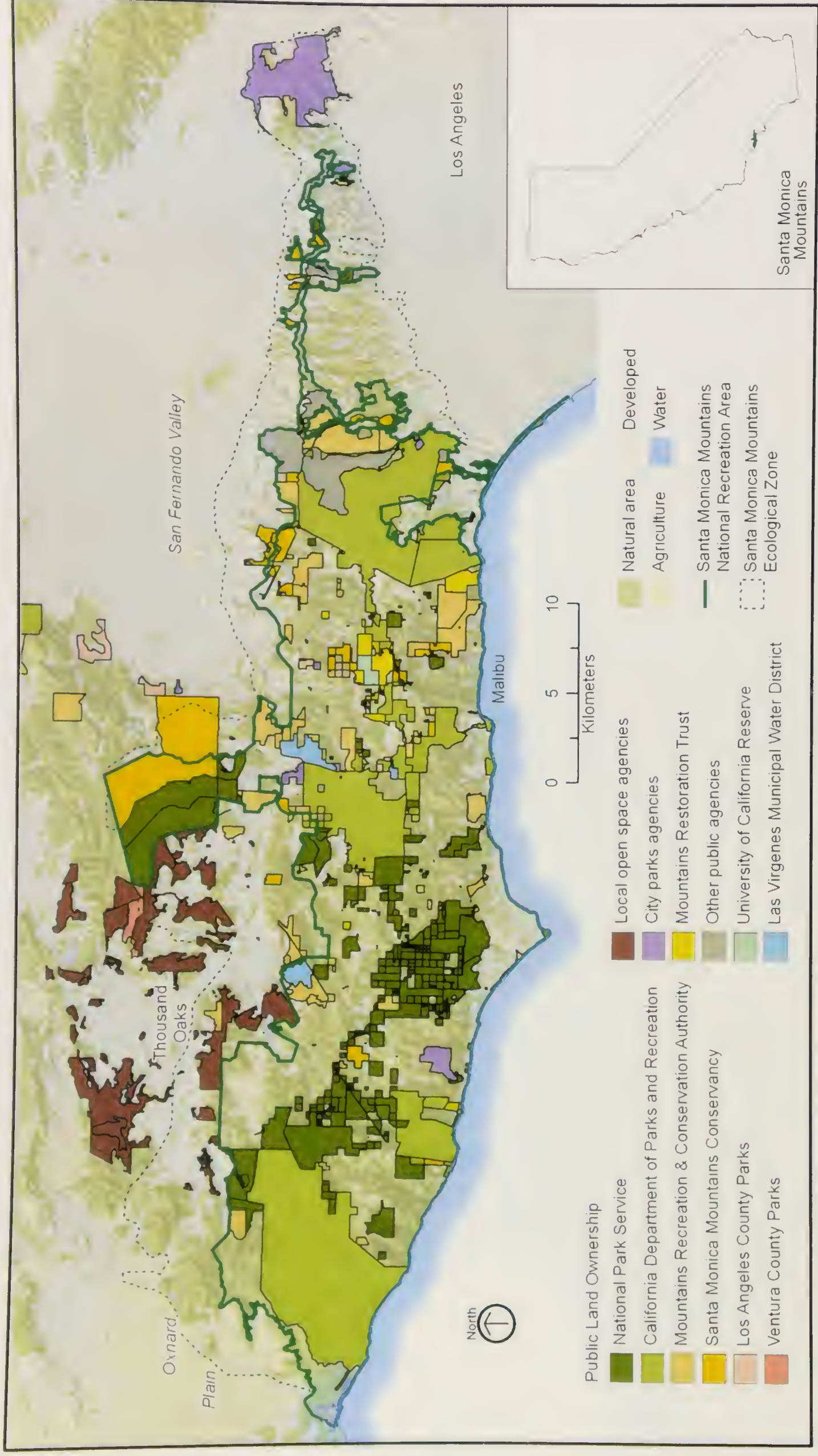
Figure 3. *Public Land Ownership in the SMMNRA.* Public land ownership is divided between numerous local, state, federal and non-profit land conservancies. This complex matrix of land ownership makes management of rare plants across the landscape challenging.
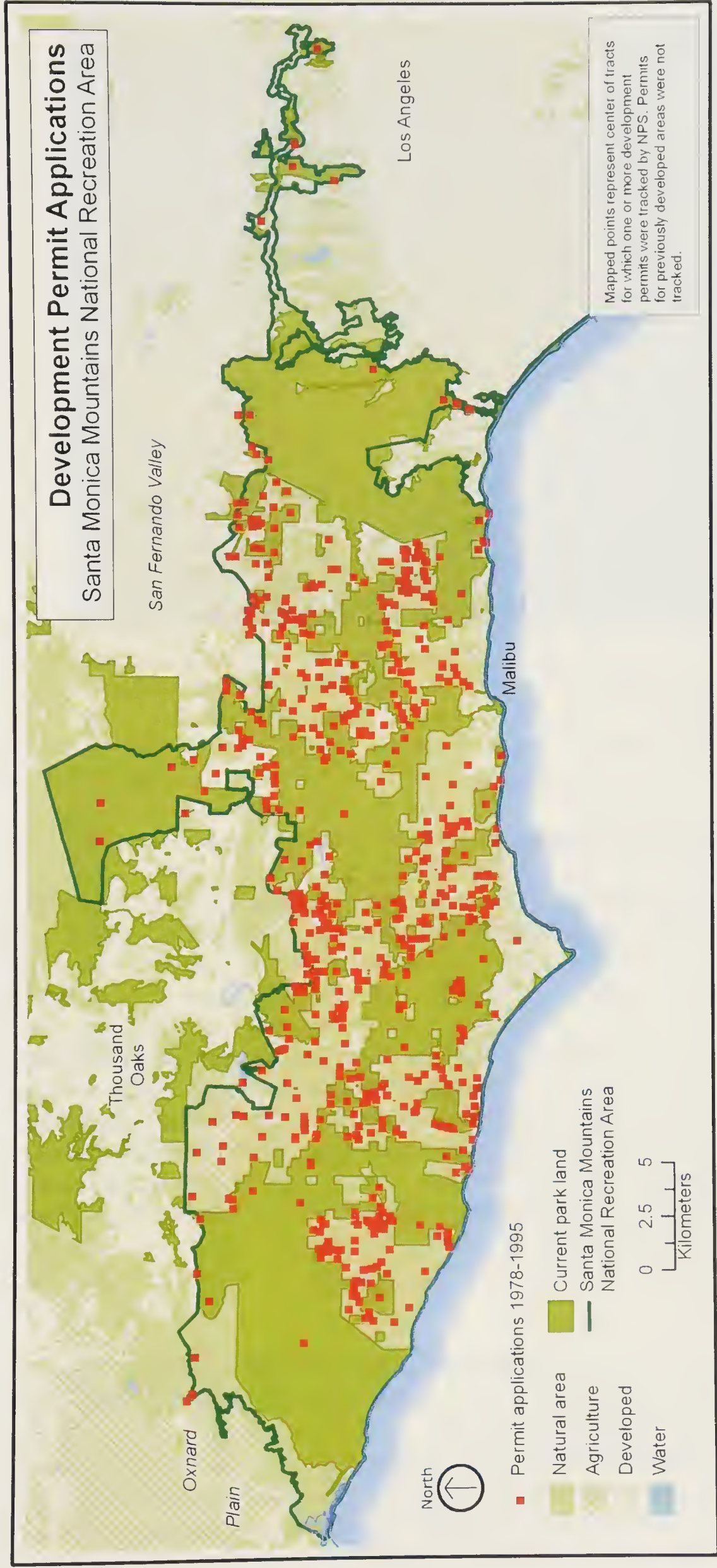
Figure 4. *Development Requests Within the SMMNRA.* Requests for development occur throughout the SMMNRA. Future development is a clear threat to maintaining biodiversity within the recreation area. Data shown is from 1978 to 1995.

Figure 5. *The Wildland-Urban Interface.* Development within the SMMNRA often occurs immediately adjacent to open space. This interdigitation of natural and developed areas can lead to impacts to rare and endangered plants in open space areas adjacent to development.

Conservation Challenges to Rare Plant Conservation at the Wildland-Urban Interface

In trying to conserve rare plants at the wildland-urban interface, managers face both ecological and organizational challenges. Although many of the ecological challenges to rare plant persistence in urban landscapes are similar to those of species in less developed environments (such as habitat loss), these issues tend to be exacerbated by the influences of urbanization. Factors such as high visitation rates, large amounts of wildland-urban edge, and high movement rates of people and goods through the environment influence how habitat loss and fragmentation affect populations. The context of an urban landscape matrix also presents some unique stressors unlikely to be experienced by rare plants in other environments, including high nitrogen deposition rates and ecological influences of neighboring landscapes. Management challenges at the wildland-urban interface include conflicting management goals and practices among agencies, difficulty of coordinating management and conservation efforts between groups and areas, and a lack of consistency in population or habitat sampling.

Ecological Challenges

Managing rare plants at the wildland-urban interface poses a number of challenges due to the proximity of development and the myriad direct and indirect effects of development, habitat loss, and habitat fragmentation on plant biology and ecology (Figure 6). The clearest direct impacts are due to population loss from habitat development, while the potential indirect effects of this habitat loss include habitat fragmentation leading to possible loss of genetic diversity, impacts on seed production, and inability to respond to fluctuating environmental conditions.
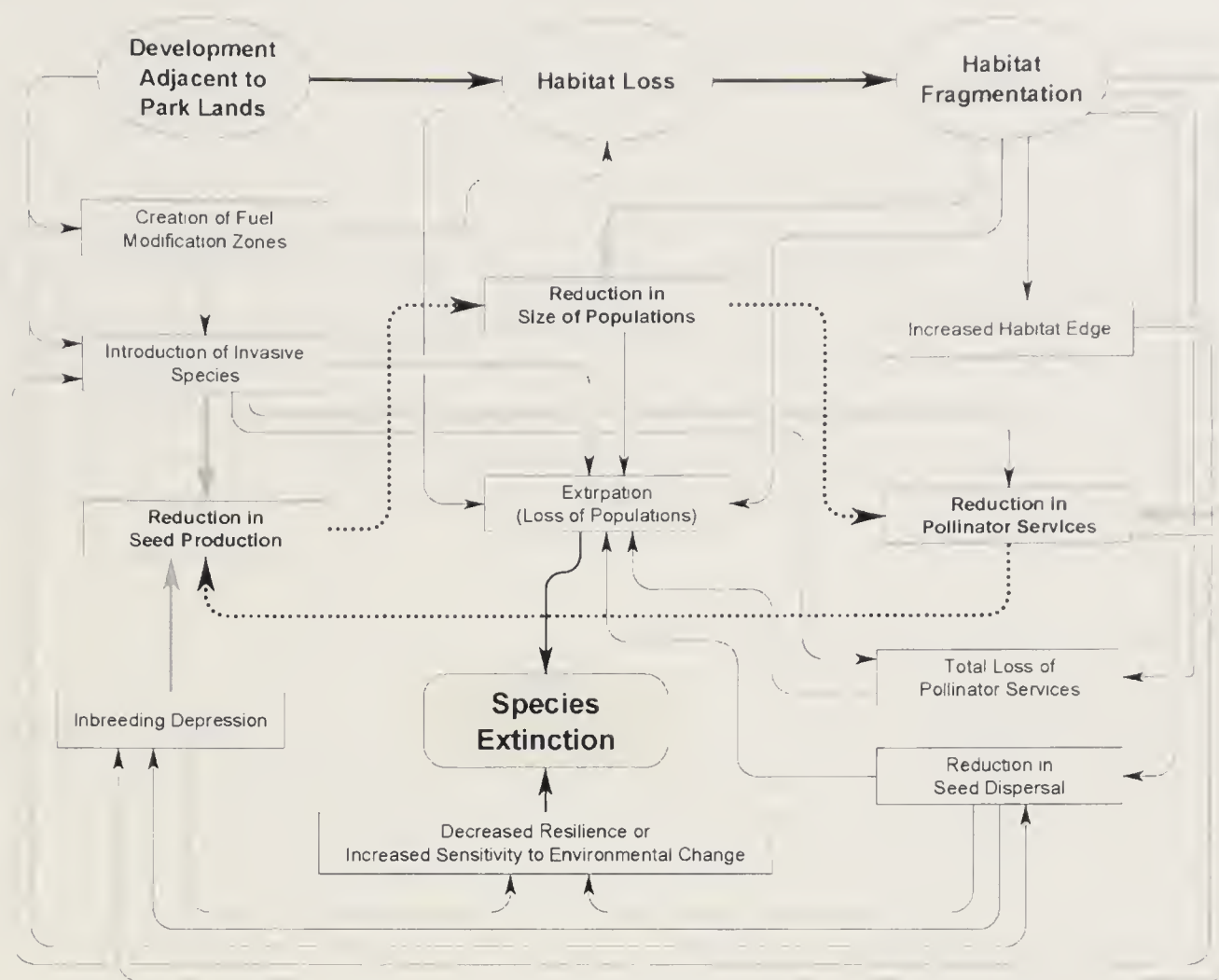
Figure 6. *Direct and Indirect Impacts of Urbanization on Rare Plant Populations.* Note that each primary driver, habitat loss, habitat fragmentation, and development has numerous direct and indirect impacts on rare plant populations. Of particular importance are feedback loops such as the reductions in population size leading to reductions in pollinator service leading to reduced seed production and further reductions in population size. Such feedback loops may eventually lead to population extirpation and eventually species extinction.

Habitat Loss

The most straightforward impact of the wildland-urban interface on rare plant species is direct habitat loss due to development. In the eight years since the writing of the recovery plan for *Pentachaeta lyonii*, National Park Service survey data indicates that 17% of the known California Natural Diversity Database occurrences have been lost due to development and an additional 10% were extirpated on public land, for a total population loss to date of 27%. Seventy percent (21 of 30) of the current known occurrences are on private land and are thus subject to possible loss to development in the future. Only 30% (9 of 30) occurrences are on protected public property. It is unlikely that this small number of populations will be sufficient to ensure survival of the species over the long-term.

The potential ecological impacts of habitat loss include a reduction in the genetic diversity of the species, reduced buffering with respect to environmental change, and greater susceptibility to extinction due to chance events. A large body of theoretical work demonstrates that species with fewer populations are more susceptible to extinction due to catastrophic events (e.g., May 1973, Roughgarden 1975). In addition, loss of a single population can lead to a feedback loop of population loss if the species has source-sink dynamics (Harrison 1991). Loss of a single population that is a source for other nearby populations can lead to further population loss. Even

in cases where the population destroyed is not a source population, population loss still results in fragmentation of the existing populations and less connectivity between remaining populations. The ultimate result of continued loss of individual populations is species extinction.

Habitat Loss- Fuel Clearance

Due to high fire frequencies in the Santa Monica Mountains, local fire departments require that homeowners clear between 100 and 200 feet of vegetation around their homes (the exact clearance distance depends on particulars of county and city fire regulations, slope, and vegetation type). In many areas within the Santa Monica Mountains this fuel clearance is conducted on public nature preserves because the private landowner has built their home immediately adjacent to the property line. At two of the eight publicly owned *Pentachaeta lyonii* sites this fuel clearance results in taking hundreds of individual plants every year prior to seed production (J. Pucci, pers. comm.).

Habitat Loss – Type Conversion

Habitat loss can also result from conversion of appropriate vegetation types to plant communities that do not support threatened and endangered species. In southern California, increased fire frequencies due to human-caused fire ignitions have resulted in type conversion of shrub-dominated habitats to non-native annual grassland (see review in NPS 2005 and Witter, Taylor and Davis, this volume), which do not support any of our threatened or endangered plant species.

Habitat Fragmentation-Pollination Impacts

Loss of populations on private lands and development of natural areas between populations can result in habitat fragmentation and isolation of rare species across their limited range. This fragmentation has the potential to impact both pollination rates and pollen movement between populations. Impacts on pollination may result from increasing population isolation, decreasing population size, changes in the habitat matrix between populations, or a combination of all three factors.

Previous research has shown that increasing population isolation can reduce pollination in plants (Groom 1998). This has troubling implications for obligatory outcrossing rare plant species such as *Pentachaeta lyonii* (Braker and Verhoeven 2000, Fotheringham and Keeley, 1998). The maximum distance that different pollinator species will travel between either individual plants or habitat patches is unknown. This distance will vary from species to species and may depend on the type of habitat being traversed. Data on bumble bees (*Bombus terrestris*) suggest that they may travel long distances from their nests (up to eleven kilometers) to floral resources if the pollen reward is sufficiently high (Walther-Hellwig and Frankl 2000). For species with extremely scattered distributions, unoccupied natural habitat between populations may act as migration corridors for pollinators. *Pentachaeta lyonii* is thought to be pollinated by generalist pollinators that also feed off of the nectar and pollen resources of other native species (Braker and Verhoeven 2000, Fotheringham and Keeley 1998). Conversion of natural habitats to urban developments with fewer or different floral resources may prevent pollinators from moving through the landscape and accessing isolated *Pentachaeta lyonii* patches.

Further reductions in pollinator service may result from declines in population size and conversion of surrounding habitats due to urbanization (see review in Kearns et al. 1998). If stresses from development (e.g., direct habitat loss, changes in hydrology, invasion of non-native species, trampling) reduce plant population size, pollinator service to that patch may be

jeopardized. Several studies have shown decreases in pollinator service with decreasing population size (Jennersten 1988, Agren 1996, Morgan 1999).

The effectiveness of pollinator visitation can also be affected by fragmentation and development. If insufficient numbers of a rare species occur within a site, generalist pollinators may visit other species and the stigmas of the rare species may become clogged with foreign pollen (e.g., McLernon et al. 1996). This can result in a lack of seed set and, over time, cause population declines (e.g., Randall and Hilu 1990). There is the potential for ornamental plantings adjacent to natural areas to generate large loads of foreign pollen and negatively impact pollination of rare species in adjoining natural areas. Foraging patterns of pollinators in a wildland-urban mix and the impacts of these patterns on reproduction of native plants is currently unknown. Reduction in habitat size and alteration of surrounding landscapes could also alter pollinator assemblages, additionally affecting pollinator service (Kearns et al. 1998).

Planting of ornamental vegetation is only one of many possible impacts of development on habitat for pollinators. Increasing water availability due to irrigation can also have large impacts on pollinator habitat. Previous studies have shown that irrigation increases Argentine ant invasion with subsequent negative impacts on native arthropods (Suarez et al. 1998). Pollinators need nesting, foraging, egg-laying, pupation and overwintering sites (Xerxes Society 2003); all of these may be compromised by development. In addition, the use of pesticides by homeowners can have negative impacts on native insects in the area (Xerxes Society 2003).

All of these potential impacts on pollination are cause for concern in rare plant species. Reductions, loss, or alterations in pollinator service will impact both seed production and, potentially, population size. There is also an opportunity for a negative feedback loop in pollinator service with reduced pollination leading to reduced seed production and reduced population size leading to further reductions in pollination. Immediate reductions in population size may not be seen during surveys, especially for perennial species. Reductions in seed production will, however, impact the population over the long-term through reductions in the seed bank or fewer individuals recruiting into seedlings and subsequent small size classes. In addition to direct impacts on seed production and (potentially) population size, disruption of pollination may also have long-term impacts on the genetic diversity of the population. These impacts are discussed later under genetic effects.

Habitat Fragmentation- Impacts on Seed Dispersal

Assuming pollination occurs, rare plant biology can still be disrupted at the seed dispersal stage. The dispersal mechanisms of the twelve state- or federally-listed species in the Santa Monica Mountains are unknown but some inferences can be drawn from seed appearance (Table 1). These twelve species show a mix of biotic and abiotic dispersal modes. Animal dispersal, wind dispersal, and water dispersal all have the potential to be disrupted by habitat fragmentation. Animal movement between rare plant populations may be reduced if roads and developments are introduced between habitat patches. Many studies have demonstrated the impact of roads on animal movement (see review in Forman and Alexander 1998).

Abiotic dispersal mechanisms can also be disrupted by development. Movement of water in urban or suburban developments is severely altered compared to what would have occurred in the natural landscape. The addition of hardscaping (sidewalks, roads, roofs, and other impervious surfaces) eliminates infiltration into the soil, and increases the velocity at which water travels. In addition, water in these developments is typically channeled along the roadsides and V-ditches or into drainage systems that drain to a stream or engineered basin. This can interrupt percolation

and natural sheet flow that normally occurs across the landscape. These changes suggest that seed dispersal of rare plants from populations that abut developed areas may be disrupted. Buildings and other facilities associated with development also have the potential to change wind patterns and disrupt movement of wind-dispersed species.

Seed movement between populations may be particularly important for rare plant species that rely on temporally variable habitats. Both *Pentachaeta lyonii* and *Astragalus brauntonii* (Braunton's milk vetch) appear to rely on infrequent events to produce large populations. *Pentachaeta lyonii* populations can be classified into three types: stable, transient, and infrequent. Stable populations occur on sites where soils are thin or where volcanic clays are very heavy and deep, resulting in reduced competition from other plant species. These populations occur in the same areas, year after year. Although the size of these populations may fluctuate by orders of magnitude in response to yearly rainfall (Figure 7), there is typically a dependable aboveground population. Transient, or satellite, populations occur on sites in proximity to larger occurrences, are small, and often appear in response to small-scale disturbance that removes other plants, such as landslides, trails, or fires. These populations last on a particular site until other plants return and canopy closure occurs. Infrequent populations are only seen above ground in high rainfall years. These large populations persist in sites that are suitable under good conditions but are mainly present as a below ground seed bank that only produces plants in amenable rainfall years.

Astragalus brauntonii shows similar patterns of population size and duration, and is also responsive to vegetation clearing disturbances. Large populations often occupy sites with appropriate soil conditions (typically carbonate soil types) following wildfire. Many of these post-fire populations decline rapidly after fire with as much as 50% loss per year (B. Landis, pers. comm.). In some sites post-fire populations can last for over ten years if abiotic conditions are favorable (B. Landis, pers. comm.). Persistence as seed in the soil is critical to the survival of this species in an environment that only exhibits low competition for brief intervals of time.

For both of these species, the ability to distribute seed widely throughout the environment in order to colonize sites following an appropriate disturbance may be key to long-term persistence. Fragmentation of these habitats with roads, development, and even small-scale agriculture has the potential to seriously disrupt the ability of these plants to disperse and utilize appropriate disturbances when they occur on the landscape.

Disruption of seed movement between populations can also result in an inability to re-colonize extirpated sites. For example, if a given population is lost due to a catastrophic event (e.g., wildfire, bulldozing during fire fighting, slope failure), the site could fail to be re-colonized due to either a lack of available seed from neighboring populations or a lack of seed movement as a result of dispersal interruption.

Habitat Fragmentation- Genetic Impacts

If pollen and seed movement are disrupted, a number of significant effects can occur over time. Genetic diversity may be lost from the population, which can result in a decreased ability to respond to a changing environment (Ellstrand and Elam 1993). Increased levels of inbreeding can occur, resulting in an increased load of deleterious alleles within a population and potentially inbreeding depression (reviewed in Ellstrand and Elam 1993). Inbreeding depression may manifest as a reduction in flower production, pollen viability, seed viability, or seedling survivorship. Inbreeding depression has been found in several rare plant species (e.g., *Arnica montana*, Luijten et al. 1996; *Aster kantoensis*, Inoue et al. 1998; and *Gentianella germanica*, Fischer and Matthies 1998).

Habitat Fragmentation- Non-native Invasive Species

Landscape fragmentation can have other impacts on remaining populations beyond pollen flow and seed dispersal disruptions. Development around preserved areas can result in large amounts of habitat edge and low amounts of interior habitat, especially for small sites. Six of the National Park Service's (NPS) thirteen park sites within the SMMNRA are under a thousand acres in size. In addition to the boundary edge of these properties, they are bisected by numerous fire roads, fuel breaks, and recreational trails. All of these edges allow points of entry for non-native species into native habitats (Rundel and King 2001, Merriam et al. 2006). The disturbed areas along trail edges and roadways serve as perfect establishment sites for non-native species traveling on boots, tires, or other dispersal agents. From these initial sites, some non-native plant species are able to move into native habitat and displace sensitive native species. Field surveys of extant versus extirpated *Pentachaeta lyonii* sites indicate that site dominance by non-native annual grasses may be a strong contributing factor to population extirpation on protected lands (J. Pucci, personal communication). All of the *Pentachaeta lyonii* populations that NPS has surveyed on public lands (all known element occurrences) have been colonized by non-native species known to compete with this rare plant (Table 2). The extent of site colonization varies between populations (Table 2) with some sites containing a high percent cover of non-native species and others containing only trace amounts.

In addition to disturbance-mediated invasion, development can also aid non-native plant invasion through propagule supply of invasive plant species. Many species that are planted in yards and developed areas adjacent to park sites have the ability to invade wildlands and displace sensitive species. The majority of invasive plant species in the United States are the result of deliberate introductions through horticulture (Reichard and White 2001), and new horticultural species continue to be introduced. Invasive species such as *Vinca major*, *Tropaeolum majus*, and *Pennisetum setaceum* are frequently planted in developments adjacent to wildlands in the Santa Monica Mountains. These species are also found colonizing adjacent natural areas and displacing native plant species. Two other landscaping species that have been directly observed invading rare plant habitats are *Schinus molle* (California peppertree) and *Gazania rigens* (gazania) (M. Meyer, pers. comm.). Thus landscaping in developments adjacent to wildlands can have direct negative impacts on habitat quality and our ability to protect rare plant species.

There can also be interactions between fire prevention activities and non-native species invasion. Many fuel modification zones are treated by either repeat mowing or disking. Both of these activities are repeat disturbances, which can create ideal conditions for non-native invasive species colonization. Fuel clearance activities frequently take place either too early or too late in the season to prevent reproduction of non-native invasive species in these areas. Thus fuel modification zones frequently serve as sources of invasive species seed and result in spread of weeds into neighboring intact habitats (Merriam et al. 2006).

Invasions of rare plant habitats by non-native species have the potential to: increase competition for resources resulting in decreased seed production; alter ecological processes such as herbivory, pollination, nutrient cycling, and disturbance regimes; and extirpate populations. Several studies have documented the negative effects of competition with non-native species on rare plants (e.g., Huenneke and Thomson 1995, Thomson 2005) and large-scale environmental changes due to non-native species invasions, such as alteration of fire regimes (see review in Brooks et al. 2004). The potential changes in biotic processes such as pollination and herbivory are less well studied.

Table 2. *Non-native species occurring at high abundance at Pentachaeta lyonii sites.* For each population location (element occurrence) each listed non-native is abundant at the site. In parentheses is listed the actual percent cover of the non-native species in 0.25 meter square plots containing *Pentachaeta lyonii.* Surveys where the non-native species was noted in the site but not found in survey plots are denoted with N.P. (not in plot). Data is from NPS population surveys in 2004.

Element Occurrence	Location	Non-native Species Present
010	Westlake Decker Canyon	Annual grass (19), *Centaurea melitensis* (1)
011	Westlake Village	*Centaurea melitensis* (1), annual grass (2), *Erodium* sp. (1)
024A	Sidlee Road	Annual grass (21)
024B	Sidlee Road	Annual grass (25)
027	Triunfo Open Space	*Centaurea melitensis* (4), annual grass, *Erodium* sp.
006	Rocky Oaks	Annual grass, *Erodium* sp., *Centaurea melitensis*
035	Malibu Creek State Park	*Erodium* sp. (3), Annual grass (2)
N/A	Tierra Rejada A	*Centaurea melitensis* (14), *Erodium* (5), Annual grass (11)
N/A	Tierra Rejada B	Annual grass (32), *Centaurea melitensis* (4), *Erodium* sp. (4)
N/A	Tierra Rejada C	*Erodium* sp. (18), *Centaurea melitensis* (3), Annual grass (N.P.)
012A	Wildwood Park	*Erodium* sp. (4), Annual grass (N.P.), *Centaurea melitensis* (N.P.)
012B	Wildwood Park	*Centaurea melitensis* (9), *Erodium* sp. (N.P.), Annual grass (N.P.)
012C	Wildwood Park	*Centaurea melitensis* (3), *Erodium* sp. (N.P.), Annual grass (N.P.)
107	Mulholland Drive	Annual grass (34), *Centaurea melitensis* (N.P.), *Erodium* sp.(N.P.)

Rodent populations may increase due to increased food availability provided by non-native species such as annual grasses and mustards. In addition, these non-native plants provide cover to rodents from predation and can result in high herbivory rates on native species (M. Witter and J. Orrock, unpublished data).

Disruption of Water and Nutrient Cycling

Invasions of non-native plant species into wildland areas at the urban-wildland interface can also be facilitated by unnatural hydrology. In the semi-arid Santa Monica Mountains, the majority of streams are seasonal, with above-ground flow only occurring during the winter and spring months. In general, riparian areas are prone to invasion by non-native plant species due to their high natural rates of disturbance (soil movement, ground clearing during flood events), large amounts of propagule movement, and more mesic growing conditions. The natural summer drought of the Santa Monica Mountains' streams can act as a barrier to colonization of riparian areas by non-drought tolerant invaders. Unfortunately, the seasonal nature of several streams in the Santa Monica Mountains appears to have been altered due to large amounts of urban run-off reaching streams during the summer months from irrigated landscaping adjacent to park sites. Evidence from historic photographs and personal accounts indicate that several streams within the

Santa Monica Mountains are now permanent when they were once ephemeral. Streams supplemented with large amounts of urban run-off appear to have greater numbers of non-native invasive plant populations. Research is currently underway to clarify the amount and timing of run-off into streams and identify whether non-native invasive plant species utilize these nuisance flows to survive during the summer drought (R. Gebauer, pers. comm.).

Unnaturally high levels of soil nitrogen due to deposition from polluted urban areas can also disrupt ecosystem functioning in natural areas. Increased nitrogen from atmospheric deposition has been implicated in the conversion of coastal sage scrub to grassland and the invasion and spread of non-native plant species in general (Allen et al. 1999). Fugitive dust from nearby construction can also alter growing conditions by increasing fine particles in poor soils, increasing water holding capacity and generating more favorable growing conditions. For rare taxa that are poor competitors and favor sparsely vegetated growing conditions, atmospheric fertilization and other soil amelioration effects may speed succession and result in the loss of favorable growing sites.

Management Challenges

In addition to the ecological challenges posed by the wildland-urban interface, there are also a number of logistical challenges to managing plants in a complex matrix of public and private lands. It is difficult to coordinate management and monitoring efforts across local, state, and federal agencies. Even when all three sets of agencies agree that conserving state- and federally-listed endangered species is a priority, the ability to collect compatible data and reach consensus on management actions is often difficult.

Regulatory Challenges – Habitat Loss

One of the major challenges of managing rare plants at the wildland-urban interface is an inability to prevent habitat loss to development. Although some species with limited distributions are listed as endangered or threatened under the federal Endangered Species Act, this listing provides little protection for plants occurring on private property. Additional protections are afforded to plants that are state listed as threatened or endangered where they occur on private lands. The California State Endangered Species Act prohibits the taking of listed plants on both public and private property, however, incidental take as part of otherwise lawful development activities are permitted. Development impacting state listed species involves consultation with the California Department of Fish and Game to determine if an incidental take permit will be issued, how projects should be re-designed, and appropriate mitigation plans for any proposed harm to listed species. In addition, under the California Environmental Quality Act (CEQA), any impacts to biological resources must be mitigated to less-than-significant levels.

Under the federal Endangered Species Act, plants on private property are not protected unless there is a connection to a federal agency issuing a permit or funding the development project and the United States Fish and Wildlife Service (USFWS) determines that the project may jeopardize the continued existence of the species. In many cases, this federal nexus is a requirement for a permit from the Army Corps of Engineers or receipt of federal funds for part or all of a project (e.g., road development, power plants, or other infrastructure projects). Even in cases where there is a federal nexus on a private development project, the project is often allowed to go forward with either minor redesigns to avoid direct impacts to the plants or with funds set aside for habitat mitigation. A recent economic analysis of the proposed critical habitat designation for *Pentachaeta lyonii* makes note of only a single project re-design in response to its presence in the nine years since the species was federally listed (CRA International 2006). In contrast, there have

been at least three substantial project re-designs to protect *Pentachaeta lyonii* on private lands due to implementation of the California State Endangered Species Act.

The effectiveness of project redesign vs. required or regulated mitigation in protecting endangered plants from development impacts has not been quantitatively analyzed. I have observed several problems with these two approaches to plant conservation. In the first case, where development is allowed surrounding an endangered plant population but not directly on top of the plants, many indirect impacts occur to the populations over time, resulting in long-term population declines. Development immediately adjacent to the populations can change the hydrology of the area, which can make the habitat unsuitable for the endangered species. Further impacts of development include trampling from recreational use and domestic animals, invasion of non-native plants from adjacent properties, and plant destruction due to fuel modification activities required on lands directly adjacent to development. *Pentachaeta lyonii* populations at two publicly owned sites (one in Ventura County and one in Los Angeles County) lose plants prior to seed production every year as part of fuel modification clearance activities required by local Fire Departments. A *Pentachaeta lyonii* preserve in the Simi Hills is closed to the public but several unauthorized social trails bisect the habitat area. Many invasive species are also present at this site and there is insufficient funding for ongoing management. In addition, management of the preserve is complicated by the involvement of the Homeowners Association, maintenance districts, and other interested parties.

Inconsistent Monitoring

Within the Santa Monica Mountains, monitoring efforts have been duplicated for one species (*Pentachaeta lyonii*), while there is a complete lack of monitoring data for other species (e.g. *Dudleya* sp.). This lack of consistency comes from a lack of time and personnel to carry out management and monitoring activities, let alone to meet with other agencies and discuss a unified monitoring and management strategy. These inconsistencies hamper our ability to detect trends in population sizes in these species and to respond appropriately to demographic trends by initiating management actions. Rare plant habitats are being over-run by non-native species and rare species populations are declining on public lands both because we are monitoring with insufficient frequency to detect these changes and because we lack the funding, information, and consensus necessary to treat non-native plant populations where they occur with endangered plants.

National Park Service *Pentachaeta lyonii* population surveys over the past four years indicate that at least three populations on public lands have been extirpated and that existing populations show large yearly fluctuations (Figure 7). While the plant's populations most likely fluctuate naturally in response to environmental conditions, it is difficult to assess whether current fluctuations are outside of the natural range of variability due to the lack of long-term data on population size. In addition, these large fluctuations mean that tens of years of monitoring data will be required to generate a reliable population viability analysis for known populations (see review in Brigham and Thomson 2003). It is difficult to generate such a dataset when funding for endangered plant monitoring is scarce and survey efforts by all agencies are inconsistent.
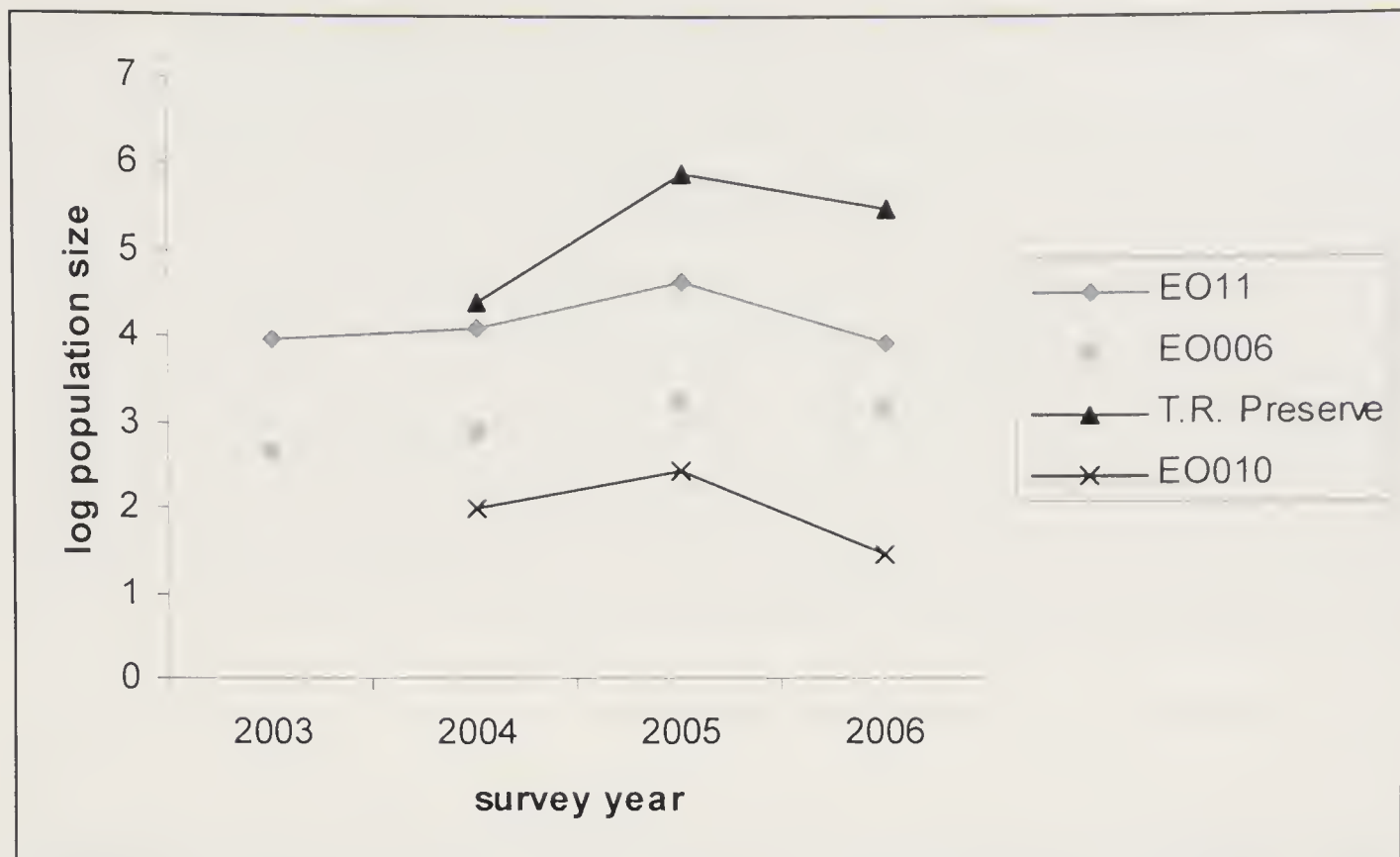
Figure 7. *Survey Data for Pentachaeta lyonii.* Note the large fluctuations in yearly population size. Both large and small populations fluctuate wildly. E.O.010 had a population low of 29 plants in 2006. It is unclear whether these populations will persist over the long-term. These large fluctuations make generating an accurate population viability analysis difficult and hamper management decision-making.

Lack of Jurisdiction

Land managers and regulatory agencies often lack jurisdiction over endangered plant occurrences on private property (although this is not true for species listed under the California State Endangered Species Act). This lack of regulatory authority means that more effort must be put towards education and voluntary compliance with species conservation efforts. The effort required to reach private landowners is magnified in an area like the Santa Monica Mountains where landowners are distributed across seven municipalities and over 250 homeowner groups.

An additional impact of the lack of jurisdiction is the challenge of tracking population dynamics when the majority of the species' occurrences are located on private property. Private landowners are often not keen to have surveys of rare plants conducted on their property when they perceive the known presence of such a species to be an impediment to future development (and thus the value) of their property. Although such surveys are often required prior to development, these surveys typically provide insufficient information since many of our rare species only appear above ground in response to appropriate environmental conditions (post-fire, good rainfall year, etc.). Thus for the majority of our rare species we have incomplete knowledge of where they occur on the landscape and what the year to year population sizes are for known occurrences. This lack of information hinders management and conservation decision-making.

Difficulty of Monitoring and Commenting on Development

Managing rare plants in an environment with ongoing development pressures presents unique challenges. Although habitat loss due to development is not a condition unique to the wildland-urban interface, the large numbers of permits and their distribution across the landscape is a

function of the encroachment of the urban edge into wildlands (Figure 5). One of the roles of the NPS is to provide input to local planning agencies on how proposed developments may impact park resources. Potential resources that might be impacted include threatened and endangered plants, viewsheds, air quality, noise, visitor experience, water quality, watershed quality, and wildlife corridors, to name just a few. It is difficult to comment on all of the possible development projects that may impact park resources due to both the sheer number of proposed developments within a year and the lack of quantitative data on possible impacts to park resources. Within a single year, NPS receives hundreds of notices of proposed developments within the SMMNRA boundary. Of these hundreds, we review approximately a hundred projects a year and write formal comment letters for approximately 40 projects a year. Our lack of understanding of the ecological impacts of fragmentation and adjacent development on rare plants, as discussed in the ecological section above, severely hamper our ability to elucidate what the impacts of proposed developments will be on rare plants.

Lack of Coordinated Management Plans and Actions

An additional challenge for managing rare plants at the wildland-urban interface is our inability to manage both populations and threats on a landscape scale. The juxtaposition of both large and small private inholdings throughout the landscape prevents us from managing plants on a landscape level. For example, at the NPS Paramount Ranch property we are trying to prevent *Centaurea solstitialis* (yellow star thistle) from colonizing *Pentachaeta lyonii* habitat. Large stands of *C. solstitialis* occur on the property and we are in the process of treating these infestations. Unfortunately, *C. solstitialis* has also become established along county roads in the area. We are working with the county through the Los Angeles County Weed Management Area to treat these roadside populations, but both lack of funding and difficulty coordinating the timing of repeat treatments interfere with our ability to control roadside infestations. In addition, numerous *C. solstitialis* infestations are present on private property in the area. These limitations on our ability to remove all seed sources forces us to manage each piece of property as an ecological island while at the same time continuing to work with local agencies and land owners to try to eliminate seed sources on non-NPS properties.

OPPORTUNITIES IN THE WILDLAND-URBAN INTERFACE

While working in the wildland-urban interface exacerbates many challenges to conserving rare plants, it also generates unprecedented opportunities for both education and conservation. Our park is embedded within the largest metropolitan area in the United States. Over 30 million people visit the SMMNRA each year. This is a large audience for conservation messages and outreach activities. It is important that these constituents have opportunities to interact with and appreciate biodiversity and open space. The SMMNRA provides venues for urban southern Californians to recreate within and come to appreciate the California Mediterranean Ecosystem. If these constituents do not value our natural heritage, including our threatened and endangered plants, then future conservation bills, environmental legislation and preservation bonds will fail and funding and public support for conservation will fade away.

Volunteerism

The large population within easy reach of our park results in a large pool of volunteers. We have had great success working with high school students from the Los Angeles Unified School district to restore degraded habitats within the SMMNRA. Each year over 2,000 students plant over 4,000 native plants at various sites throughout the mountains. In addition, the California Native Plant Society (CNPS) works at sites throughout the Santa Monica Mountains to remove

non-native species and plant native plants. California State Parks and NPS have both benefited from the tireless stewardship of CNPS volunteers. Additionally, local botanists and environmental consultants are often experts on certain species or groups. Betsey Landis, a local botanist and CNPS past chapter president, is the local expert on *Astragalus brauntonii*, having studied aspects of its biology as diverse as soil preferences and herbivory. Although NPS staff has discussed the idea of having small volunteer groups adopt a *Pentachaeta lyonii* occurrence or a *Dudleya* patch and keep it weed-free and carefully tended well into the future, we have yet to identify appropriate groups for such an activity or to test this idea on the ground. NPS research has shown that hand weeding *Pentachaeta lyonii* plots can increase its performance (NPS unpublished data). This type of work is time-consuming and labor-intensive. It can be difficult to work within rare plant populations due to the small size and delicate nature of individual plants. A group selected for rare plant conservation would have to be rigorously trained and extremely meticulous in order to avoid the possibility of trampling a population into extirpation.

Pooling Agency Resources

Another opportunity arises from the large number of local non-profit, state, and federal land management agencies that are active within the wildland-urban interface of the SMMNRA. With so many management agencies, we have many opportunities to pool our resources to achieve important goals. The National Park Service works with partners on many of our natural resource and education projects. For example, our school restoration program described above is a joint program between NPS and a local land trust, the Mountains Restoration Trust. The three major public landowners in the Santa Monica mountains, the California Department of Parks and Recreation, the National Park Service, and the Santa Monica Mountains Conservancy, recently pooled funds to purchase Gillette Ranch, a 500-acre park area in the heart of the mountains. There is the potential for a similar type of collaboration to occur concerning rare plant management across the mountains. While public bond monies often provide funds for land purchase, monitoring and management is typically under-funded across all agencies. Although none of the agencies individually has sufficient funding to hire a dedicated rare plant botanist, if funds were pooled across agencies there might be adequate funding to create such a position for a Santa Monica Mountains. This person could coordinate monitoring and management across all public lands within the mountains.

Academic Involvement

In addition to numerous land management agencies within the area, there are also a plethora of both public and private universities. These institutions represent a unique opportunity to generate new information on the biology, ecology, conservation, and management of our rare and endangered plants. The NPS has a college internship program involving 10-15 undergraduate students each year in natural resource conservation and research. Past plant ecology interns have assisted with our rare plant surveys. We are currently exploring ways to involve undergraduate classes in both monitoring and management of sensitive plants and communities within the park boundaries. In addition, we are reaching out to graduate students and faculty at research universities for help in understanding the impacts of urbanization on park resources. Several current research projects on this topic are being conducted by faculty from local research institutions, while two graduate students from California State University, Northridge, have studied endangered plants in the Santa Monica Mountains (*Pentachaeta* and *Dudleya* [see Dorsey, this volume] species).

It is sometimes difficult to forge the link between basic research in a university setting and the applied research managers need to improve decision-making. Academic pressures to produce

novel publication-worthy research can conflict with the need for site-specific basic research for management questions. Involving academic researchers in management questions can sometimes require forging personal relationships or providing park datasets or grant funds for needed research. A recent National Park Service-wide initiative should help with this interface. The research learning centers of the NPS are dedicated to bridging the gap between academia, park managers, and the general public. The mission of the research learning centers is to increase the number of academics conducting research in national parks and to communicate the findings of research to the general public. The California Mediterranean Research Learning Center (CMRLC) encompasses three national parks within California: the Santa Monica Mountains National Recreation Area, Channel Islands National Park, and Cabrillo National Monument. To date, The CMRLC has funded numerous college interns to conduct research in the park as well as several academic studies, including one of *Dudleya* systematics on the Channel Islands and in the Santa Monica Mountains.

Private Landowner Conservation

A final opportunity of managing rare plants at the wildland-urban interface is the possibility of involving private landowners in species conservation. The use of conservation easements, set-asides, and tax breaks was pioneered in areas with large private landholdings such as ranches and farms, however there is no reason why this approach could not be extended to smaller parcels within the SMMNRA. Although the individual conservation value of a particular small parcel may not be very high, when the entire landscape is comprised of such parcels conserving as many of them as possible becomes an urgent matter. Working with private landowners to conserve wildlife corridors through their property, to construct backyard habitat, and to develop lands in the most ecologically friendly manner possible is essential if the endangered plants and animals of the Santa Monica Mountains are to survive. We must seek to hone our understanding of what can be done on a small scale to increase habitat connectivity, prevent weed spread, and allow for preservation of genetic diversity and population interchange among endangered plant occurrences scattered throughout the landscape.

CONCLUSION

Maintaining the entire complement of native species in the Santa Monica Mountains in the face of continuing development and extreme interdigitation of public and private lands continues to be a great challenge. Developed areas present a host of both ecological and management challenges to the persistence of the rare plants of the Santa Monica Mountains. Many of the potential ecological impacts arise from either direct habitat loss or fragmentation effects. It is unclear how severe the impacts of habitat fragmentation on our rare plants will be, but the potential for species decline, and even loss, is great. Fragmentation effects such as inbreeding depression, invasive species colonization, pollinator disruption, and dispersal limitation may take many years to reveal their true impacts. Management challenges, including the need to unify monitoring and management approaches, work with private landowners, and apply management at a landscape scale, will most likely continue to plague rare plant conservation at the wildland-urban interface.

In order to overcome these difficulties and make the most of our urban setting we need to engage the public and involve both groups and individuals in rare plant conservation. The more opportunities land managers can provide for the public to engage in conservation or restoration activities, to participate in stewardship, and to connect with their biotic heritage, the better future we will all have. Efforts we make to protect rare plants will benefit not only the rare species of interest but also many other species of plants and animals.

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A VEGETATION CLASSIFICATION FOR THE SANTA MONICA MOUNTAINS

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ABSTRACT: The vegetation of the entire Santa Monica Mountains and adjacent area north to the Simi Hills was systematically sampled to develop a detailed vegetation classification. This classification will form the basis for a detailed vegetation map and provide a baseline data set for the long-term monitoring and management of the area's natural resources. In this 320,000-acre region, over 4,100 individual vegetation surveys were allocated based on a Geographic Information Systems (GIS) biophysical model, which identified seven ecological zones defined via climatic, geologic, and topographic conditions. The California Native Plant Society (CNPS) Rapid Assessment protocol was used to obtain the majority of the data. The field data were analyzed using TWINSPAN and agglomerative cluster analysis. The final analysis relied on a set of 254 species and 3,912 samples. These samples were partitioned into 84 alliances or unique stands, 204 associations, and 73 phases. The rapid assessment method compared favorably to relevé and other methods of sampling vegetation for classification. The robustness and level of detail of the classification is unsurpassed in California vegetation classification.

KEYWORDS: Vegetation classification, Santa Monica Mountains, vegetation map, Rapid Assessment Vegetation Sampling Protocol, vegetation alliance, vegetation association, vegetation phase

INTRODUCTION

The Santa Monica Mountains and adjoining Simi Hills are not only the most accessible and largest piece of natural land adjacent to the western Los Angeles Basin but also play an important role in the panoply of vegetation in southern coastal California (Figure 1). Fire history, differences in soil, moisture, and temperature regimes, and topography all combine to create complex patterns of woodland, chaparral, coastal scrub, and grassland vegetation. The mountains

Figure 1. Topography including slope position, steepness, and exposure has a strong influence on vegetation patterning in the Santa Monica Mountains. In this view are stands of *Quercus agrifolia, Q. berberidifolia, Adenostoma fasciculatum, Ceanothus megacarpus, Ceanothus spinosus,* and *Platanus racemosa* alliances, Upper Solstice Canyon, facing southeast.

are home to several locally common but regionally restricted species (such as *Ceanothus spinosus, C. megacarpus, Eriogonum cinereum,* and *Coreopsis gigantea*); each because of its high sociability and abundance defines its own suite of vegetation types. Other alliances defined by *Encelia californica, Salvia leucophylla, Juglans californica,* and *Rhus integrifolia* are regionally distributed in southern, coastal California and display a more concentrated distribution and a broader variation of vegetation associations here than anywhere else.

The Santa Monica Mountains are the westernmost and lowest of the Transverse Ranges of southern California. They have small stands of higher-elevation chaparral alliances such as *Quercus wislizeni* var. *frutescens* and *Arctostaphylos glandulosa,* remnants of a cooler and perhaps moister climate. They also are tall enough to sustain a more extensive presence of some higher-elevation chaparral alliances such as *Ceanothus oliganthus* and *Adenostoma sparsifolium.* In addition, they contain the southernmost stands of *Quercus lobata* woodlands in California and among the largest remaining woodlands of *Juglans californica.* The seaward bases of the mountains have succulent coastal scrub like that of Baja California, including stands of *Opuntia littoralis, O. oricola,* and *O. prolifera* along with drought deciduous scrubs such as *Salvia leucophylla, Artemisia californica,* and the largely insular *Coreopsis gigantea.* The core of the mountains covers thousands of acres and includes varied examples of *Ceanothus spinosus* and *C.*

megacarpus alliances, both representing the center of their world distribution (Figure 2). Riparian vegetation includes extensive woodlands of *Platanus racemosa, Salix lasiolepis,* and *S. laevigata,* which often interface with lower slope woodlands of *Quercus agrifolia, Juglans californica,* and *Umbellularia californica.* Further south, the latter two alliances diminish significantly, thus signifying the biogeographic role of the Santa Monica Mountains as crossroads between northern and southern California coast range vegetation.

The National Park Service, Santa Monica Mountains National Recreation Area (NPS) undertook development of a new vegetation classification and map in 2001. NPS entered into a contract with Environmental Systems Research Institute, Inc. (ESRI), to develop a vegetation classification and map. ESRI subcontracted with CNPS via the California Heritage Program ecologist (housed at California Department of Fish and Game, CDFG), representing NatureServe in California. ESRI also subcontracted with Aerial Information Systems, Inc. (AIS), to produce a map driven by the classification developed by CNPS and CDFG. Primary responsibility for development of the classification was assigned to Todd Keeler-Wolf (CDFG California Heritage Program senior vegetation ecologist) and Julie Evens (CNPS senior vegetation ecologist). Edward Reyes (AIS) was the lead photo-interpreter and vegetation mapper. NPS assumed responsibility for field data collection, vegetation database management, and statistical analyses. With supervision from John Tiszler, field data were collected during a continuous two-year effort and managed by Julie Christian from 2002 to 2004.

Figure 2. The *Ceanothus spinosus* Alliance (foreground and left-center) has its center of distribution in the Santa Monica Mountains.

The primary motivation for this project was to produce a new vegetation classification and map that meet NPS and U.S. National Vegetation Classification (USNVC) standards and to provide the information base necessary to develop effective fire hazard management strategies while fully protecting natural resource values. In addition, the classification and map will have many uses for the numerous public planning and land conservation agencies with jurisdiction in the Santa Monica Mountains and Simi Hills. For example, the classification and map will provide a highly detailed spatial assessment of native vegetation and, as such, will be a valuable planning tool where habitat connectivity, sensitive vegetation types, and protection of designated Ecologically Significant Habitat Areas are of concern. The results will improve the capacity to make local vegetation management and other land-use decisions.

This article provides our methods for sampling and classification, a listing of the vegetation types defined, and a brief description of the broad ecological zones of the Santa Monica Mountains that we determined in the course of our study.

METHODS

Study Area

The area of study was the Santa Monica Mountains and its environs, including the Simi Hills and Montcleff Ridge. The area encompasses approximately 225,000 acres, from Griffith Park in Los Angeles in the east to Point Mugu State Park in the west and from Simi Valley in the north to the Malibu Coast (Figure 3). Of that area, approximately 75,000 acres is developed, including the cities of the Conejo Valley and the City of Malibu. We excluded these areas from the survey.

Standards and Protocols

This vegetation classification follows the U.S. National Vegetation Classification (USNVC) guidelines (Grossman et al. 1998). Refinements to the classification have been occurring in the application process, leading to ongoing proposed revisions that are reviewed both locally and nationally (http://www.natureserve.org/explorer/). Vegetation mapping in national parks has been undertaken under the auspices of the NPS Inventory and Monitoring Program, in close cooperation with the USGS-Biological Resources Division (BRD). The mapping is done in accordance with standards established by the Federal Geographic Data Committee (FGDC) for vegetation mapping on federal lands. The FGDC Web site (http://www.fgdc.gov/ standards/standards_publications/index_html) explains the development of the classification standards currently used for mapping and classifying vegetation in national parks. The USGS-BRD/NPS Vegetation Mapping project Web site (http://biology.usgs.gov/npsveg /standards.html) contains additional information on vegetation mapping in national parks.

This project was the first effort to extensively employ the CNPS Rapid Assessment Vegetation Sampling Protocol, which is an abbreviated plotless (stand-based) survey technique that relies on visual estimates of cover of the predominant species in each of the vegetation strata of a stand (see http://www.cnps.org/programs/vegetation /protocol.htm for full description).

This technique was selected, in addition to the standard relevé sampling protocol used regularly by the National Park vegetation programs, because of its ability to represent large numbers of vegetation stands quickly, thus increasing the sample size and range of sampling locations for all types of vegetation. This rapid assessment protocol provided an efficient way to inventory many

Santa Monica Mountains Vegetation Mapping Project

Figure 3. Study area of the Santa Monica Mountains and environs.

dense and difficult to penetrate stands of chaparral and coastal scrub, where the species indicative of particular ecological settings were primarily in the shrub layer and not in the understory herbaceous layer. It was used extensively in surveying virtually all types of vegetation in this project except for the species-rich riparian, oak, and other hardwood woodlands, coastal sage scrub, and grasslands in which relevés were conducted to augment the samples. The diversity of species and the more significant variation of understory species in these situations required a full sample of all species recorded to more accurately classify and understand the variations in these types of vegetation.

Field Sampling

The locations of stand samples were driven by a selection of representative landscapes using a biophysical model of the area (for details see full report in Keeler-Wolf and Evens 2006). A GIS analysis was conducted by park staff based on identification of driving variables for vegetation distribution. Specifically, a March solar radiation layer was separated into three classes (based on slope and aspect), then layers were classified and combined for:

    a) fire history,
    b) geology,
    c) average annual precipitation, and
    d) average maximum July temperature.

Field crews were directed to sampling locations identified through the GIS analysis and refined their sample locations based on the principles of stand homogeneity and accessibility (see CNPS rapid assessment protocol online, op cit.).

Data Analysis

The sample data set used for the classification included 3,790 vegetation rapid assessments, which were completed year-round from July 2002 to April 2004, and 122 relevé samples, which were completed from February to June 2003 (in the phenologically active periods of spring and summer). The very large number of samples collected for this project far exceeded any previous study for a given National Park unit. We used database queries to display the details of the cluster groupings on a plot-by-plot basis. This allowed us to visually inspect the relationships between species and their cover within the statistically determined groupings. Interim analysis about half-way through the field data collection allowed further re-focusing of sampling needs prior to the completion of the field work.

We used the PC-ORD software suite of classification and ordination tools (McCune and Mefford 1997, McCune and Grace 2002) for the initial analysis. PC-ORD performs a set of different multivariate analyses to place vegetation sample units (including both rapid assessment and relevé) into a formalized classification of vegetation types. Using analyses in the suite such as cluster analysis and ordination indicates similarities in species composition and abundance among samples. The data sets are inherently complex and more than one environmental axis may be correlated with the patterns of plot samples. We used a hierarchical agglomerative cluster analysis technique with Sorenson distance and flexible beta linkage method at -0.25. This technique is based on abundance (cover) values converted to seven different classes using the following modified Braun-Blanquet (1932/1951) cover categories: 1 (< 1%), 2 (1-5%), 3 (>5% - 15%), 4 (>15%-25%), 5 (>25%-50%), 6 (>50%-75%), and 7 (>75%). The majority of the species values fell within the first four cover classes. Prior to these analyses, data were screened for outliers (extreme values of sampled stands or species), and these outliers were removed to reduce heterogeneity and increase normality in the data set. We removed samples that were more than three standard deviations away from the mean and species that occurred in fewer than three plot samples using outlier analysis.

Because of the size and heterogeneity of the initial data set, we used a first-order cluster analysis to partition it into more distinct and manageable subsets of around 100–200 samples. Teams of two to three ecologists then analyzed the smaller subsets that usually included distinctly different vegetation types or habitats. We applied cluster analysis to both rapid assessment and relevé data, but analyzed these data sets separately because the species data were recorded differently (i.e., data on all species found in defined plots for relevés as compared to data on up to 20 main species found in stands for the rapid assessments). After the cluster analyses, we used Indicator Species Analysis (ISA) from the PC-ORD suite to determine which species had the highest fidelity for a particular proposed vegetation type using the statistical test developed by Dufrene and Legendre (1997).

ISAs were used to evaluate the total number of significant indicator species (p-value • 0.005) within each group level and the mean p-value for all species. The group level that had the highest number of significant indicators and lowest overall mean p-value was selected for the final community classification evaluation (McCune and Grace 2002). At this grouping level, plant community names within floristic classes were applied to the samples of the different groups.

Vegetation Type Hierarchy

Naming conventions follow the National Vegetation Classification System (Grossman et al. 1998) and the CNPS system (Sawyer and Keeler-Wolf 1995, and updates from Sawyer et al. 2007 ms). Both recognize the plant association as the fundamental unit of classification. We define an

association as a group of vegetation samples with a suite of dominant and characteristic (indicator) species identified through ISA. The membership rules were defined by species constancy, indicator species, and species cover values. This group of floristically similar samples is also correlated with a particular environmental setting, described in this effort by a summarization of the environmental variables collected at each sample location. Formal ordination of these environmental variables was not systematically conducted for all groupings, because of the generalized nature of most of the environmental data collected (see below). However, Bray-Curtis ordination (McCune and Grace 2002) was used to differentiate some groups. A set of similar associations are grouped hierarchically to the next level in the classification, the alliance. Alliances are generic units of vegetation classification, usually defined by the dominant and/or characteristic plant species in the upper layer of vegetation (Figure 4).

Figure 4. *Quercus agrifolia* (Coast Live Oak) Alliance has a broad range in understory variation defining different associations.

The environmental field data collected on rapid assessment surveys is basic and tends to focus on general "hard" variables such as elevation, slope, aspect, soil texture, geology, and so forth. Associations are usually differentiated by environmental factors as well as floristic characteristics. In vegetation, the arrangement of certain groups of species defining a category of vegetation correlates with a particular set of ecological situations, which may include "hard" or specific climatic and other environmental differences related to temperature, moisture, or soil nutrition; however, it may also imply more vague ecological characteristics such as mode, frequency, and intensity of disturbance. As definitions were developed, the data analysis team

used the correlates to ascertain environmental variables, or lack thereof, to help determine whether or not a particular cluster grouping should be ranked as an association.

As many of the vegetation types defined in this classification related to the "softer" variables that may be correlated with history following fire or other disturbance, it was difficult to draw specific, strong environmental correlations with many of the types. In cases where a group of vegetation samples appeared somewhat floristically distinct but shared the same environmental characteristics with a larger group of samples, the term "phase" was used. A phase is an informal unit of classification accommodating local floristic variation that tends to not have obvious correlations with certain environmental conditions, and is best considered a part of a more definitive association. Most defined phases are probably the result of localized variation in climate or site history associated with local relief, soil texture, geology, and fire history.

Each sample was revisited within the context of the cluster to which it had been assigned in order to quantitatively define membership rules for each association. Upon revisiting each sample, a few samples were found to be misclassified in earlier fusions of the cluster analysis, and these samples were reclassified based on the membership rules. The set of data collected throughout the study area was used as the principal means for defining the association composition and membership rules; however, existing classifications of similar vegetation elsewhere in the state were consulted to locate analogous/similar classifications or descriptions of vegetation.

ECOLOGICAL REGIONS

In the process of creating the vegetation classification and map, we defined seven broad ecological regions for the Santa Monica Mountains (Figure 5). We arrived at a determination of these zones by formal and informal means: through a Gradient Directed Sample Allocation (GRADSECT) (Austin and Heyligers 1991); analysis of the environmental factors likely to drive the distribution of the principal vegetation associations in the area (geology, precipitation, temperature, and solar insolation [based on slope and aspect]); and through the assessments of the field ecologists and photo-interpreters based on observations made during field data gathering and vegetation mapping. In addition, the GRADSECT analysis assisted in selecting survey locations in a stratified random process.

The following descriptions serve as brief characterizations of each of these seven regions. Each region is given a descriptive name based on our observations.

Region 1: Western Fog Zone (Coastal Sage Scrub on Volcanics)

General Location:	Far west end of range as hits Oxnard Plain
Ave-Hi/Low Summer Temp:	75/55 (Camarillo)
Ave-Hi/Low Winter Temp:	65/45, Records below 32
Fog Description:	Often foggy, possible year-round
Precipitation:	10–15", lower than Region 2
Geology:	Igneous > Quaternary >> Low Sedimentary
Soil:	Incomplete, Coastal Sage > Igneous Chaparral
Elevation Range:	0–1800'

Figure 5. Ecological regions identified for vegetation assessment.

Region 2: Immediate Coast (Coastal Sage Scrub)

General Location:	East-west band along immediate coast, south-facing Slopes
Ave-Hi/Low Summer Temp:	70/60 (Malibu)
Ave-Hi/Low Winter Temp:	65/50, No record lows below 32
Fog Description:	Often foggy, possible year-round
Precipitation:	15–18", higher than Region 1
Geology:	Sedimentary >> Quaternary ~Igneous
Soil:	Coastal Sage > Sedimentary Chaparral > Coastal Terrace > Sandstone Chamise/Chaparral > Igneous Chaparral
Elevation Range:	0–1500'

Region 3: Upper Elevation Santa Monica Mountains (Chaparral)

General Location:	South-facing slope of mountains, mid to top
Ave-Hi Summer Temp:	82 (extrapolated)
Ave-Low Winter Temp:	41 (extrapolated), frequent radiative freezing
Fog Description:	Mostly Spring
Precipitation:	18–23", 28" at highest elevations
Geology:	Sedimentary > Igneous >> Quaternary
Soil:	Sedimentary Chaparral ~Sandstone Chamise/Chaparral ~Igneous Chaparral
Elevation Range:	1000–3100'

Region 4: Lower Elevation Inland Santa Monica Mountains (Chaparral)

General Location:	North-facing slope of mountains, mid-lower
Ave-Hi/Low Summer Temp:	80/50 (Newbury Park), record highs in 100s
Ave-Hi/Low Winter Temp:	70/40, record lows in lower 20s

Fog Description:	Usually in Spring
Precipitation:	18"
Geology:	Igneous > Sedimentary > Quaternary
Soil:	Incomplete, Igneous Chaparral > Marine Sedimentary >> Coastal Terrace
Elevation Range:	1000–2000'

Region 5: Inland Dry (Coastal Sage Scrub)

General Location:	South-facing slope of Simi Hills, lower slope
Ave-Hi/Low Summer Temp:	90/55 (Thousand Oaks + Moorpark), record highs in 110s
Ave-Hi/Low Winter Temp:	70/40, record lows in 20s (Moorpark is a bit more mild)
Fog Description:	Spring only
Precipitation:	13–18"
Geology:	Sedimentary > Quaternary > Igneous
Soil:	Incomplete, Marine Sedimentary
Elevation Range:	900–1800'

Region 6: Simi Hills Inland (Chaparral)

General Location:	Simi Hills, mid to top slope
Ave-Hi Summer Temp:	85 (extrapolated)
Ave-Low Winter Temp:	39 (extrapolated)
Fog Description:	Spring, early Summer
Precipitation:	18"
Geology:	Almost exclusively Sedimentary >>> Igneous = Quaternary
Soil:	Incomplete, Marine Sedimentary
Elevation Range:	900–2400'

Region 7: Eastern Urban (Chaparral)

General Location:	Far east, urban
Ave-Hi/Low Summer Temp:	75/60 (Beverly Hills), record highs in 100s
Ave-Hi/Low Winter Temp:	65/50, record lows in mid 30s
Fog Description:	Spring, early Summer (clearing early in the day; extrapolated)
Precipitation:	18–22"
Geology:	Sedimentary > Igneous > Metamorphic >> Quaternary
Soil:	Incomplete, Sedimentary Chaparral/Urban Land, Urban Land
Elevation Range:	400–1750'

RESULTS

The final agglomerative cluster analyses for the classification used data from 3,912 of 4,014 sites sampled, and it included the 254 most abundant of 544 species sampled in the rapid assessments.

In total, 84 vegetation alliances or unique stands and 204 associations or phases were defined for the project. Of these, 177 types (at the alliance, association, and phase levels) have been fully described in Keeler-Wolf and Evens (2006). Rare stands that were not classified are also described.

We can summarize the vegetation of the Santa Monica Mountains area by inspecting the coarse levels of the cluster analysis. As the cluster analysis proceeds, all of the field sample data is agglomerated into fewer and fewer main clusters (envision cutting back all of the fine branches of the cluster diagram back to the main few that split off from the base). These fundamental groups

reflect their relationships to general patterns in regional climate, soil, and disturbance history and thus, show the general relationships of the entire range of vegetation types within the area. Species identified as significant indicators of these groups are those that tend to have high cover and high fidelity to these groups, and are thus often also used to name vegetation alliances. We selected the top group of 10 clusters in the data set to provide such an example (Figure 6). These 10 groups are arrayed along a complex gradient of temperature, moisture, soil texture, and disturbance history. The following brief narrative descriptions are arranged in the order in which the groups were arranged in the cluster analysis. The names of the groups are not numerically sequential, but are named based on the order in which they split from one another in the analysis. The most highly significant indicator species (p < 0.002) are listed.
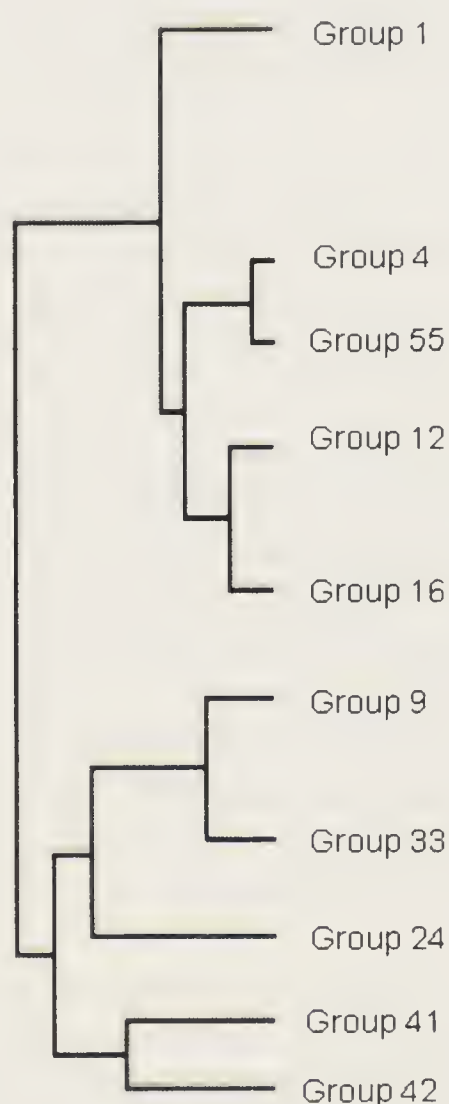

Figure 6. Cluster diagram of the 10 major groupings representing 3,912 samples. Similarity distance has been distorted to facilitate graphic representation. See text for explanation of each group.

At the most basic level, these groups are divisible into two major branches. The first group (including groups 1, 4, 55, 12, and 16 in Figure 2) includes coastal scrub shrubs and herbaceous vegetation of lower elevations, as well as wetland and riparian herbs and woody species. The second large group (including groups 9, 33, 24, 41, and 42) primarily represents the sclerophyll chaparrals and evergreen and deciduous oak woodlands.

Group 1 is made up of many species which tolerate frequent disturbance. The disturbance may be primarily fire-driven or water-driven. Many non-native herbaceous species occur here, but also

native woody species such as *Baccharis pilularis* and *Salix lasiolepis*. This group is distinct from its neighbors and represents the single largest number of samples. At a slightly finer level of division (when 13 major groups are identified instead of just 10) the wetland group separates from the non-wetland group. The following wetland species are among the significant indicators of this group: *Artemisia douglasiana*, *Baccharis salicifolia*, *Distichlis spicata*, *Frankenia salina*, *Salix lasiolepis*, *Salicornia virginica*, and *Typha* sp. The following herbaceous or early seral woody species are indicative: *Atriplex lentiformis*, *Bromus diandrus*, *Brassica nigra*, *Baccharis pilularis*, *Carpobrotus edulis*, *Foeniculum vulgare*, *Hazardia squarrosa*, *Hirschfeldia incana*, *Lolium* sp., *Nassella pulchra*, and *Phalaris aquatica*.

Group 4 represents a major part of the local coastal sage scrub vegetation characterized by drought-deciduous shrubs and associated herbs, some of which are non-native. The species in this group tend to occur at lower elevations in the maritime zone on heavy soils. Significant indicator species include: *Artemisia californica*, *Eriogonum cinereum*, *Centaurea melitensis*, and *Salvia leucophylla*.

Group 55 is related to the previous Group 4 and is composed of stands of vegetation characterized by early seral species usually associated with recent fire, within the coastal scrub zone. The most significant two indicators are the short-lived drought-deciduous shrub *Malacothamnus fasciculatus* and the perennial native grass *Leymus condensatus*.

Group 12 is distinguished by species associated with steep coastal slopes within the summer fog zone. The most significant species in this group are woody shrubs that may be drought-deciduous, succulent, or sclerophyllous. Group 12 is most closely related to the next group (16) and includes the following principle indicators: *Encelia californica*, *Salvia mellifera*, *Rhus integrifolia*, *Opuntia littoralis*, *Yucca whipplei*, and *Isomeris arborea*.

Group 16 has the widespread xerophyte shrubs *Malosma laurina* (a sclerophyll) and *Eriogonum fasciculatum* (a facultative drought deciduous shrub) as the primary indicators. This is a very well represented group locally, probably because stands dominated by its principle indicators do well with the currently prevalent high fire frequencies, and warm, well drained soils that do not experience cold winters.

Group 9 is defined by the significant presence of the major upper elevation and cold tolerant chaparral species of this region including *Arctostaphylos glandulosa*, *Cercocarpus betuloides*, *Ceanothus crassifolius*, and *C. oliganthus*. Both resprouter and obligate seeder sclerophyll shrubs are significant. These vegetation types are typical of upper slopes and/or relatively high elevations and interior locations in the region.

Group 33 is related to group 9 and has *Adenostoma fasciculatum* and *Lotus scoparius* as the strongest indicators. These are, respectively, the most ubiquitous long-lived species of the xeric upper slope chaparral, and its most characteristic early seral woody species. Other significant indicators include *Arctostaphylos glauca*, *Eriodictyon crassifolium*, and *Trichostema lanatum*. The first species is a significant member of the more inland hot summer chaparral, while the other two are early seral associates of the same settings.

Group 24 has a single very strong indicator, the chaparral shrub *Ceanothus megacarpus*. This species dominates many of the moderately xeric slopes with intermediate disturbance regimes throughout the Santa Monica Mountains, but not in the more inland Simi Hills. It is endemic to the chaparral of the south coast of California.

Group 41 is represented by resprouting chaparral shrubs or shrubby tree species which tend to occur in relatively warm but mesic settings such as northerly facing slopes throughout the region. Significant mesophyllic shrub indicator species include: *Ceanothus spinosus*, *Heteromeles arbutifolia*, *Prunus ilicifolia* and *Rhus ovata*. This group also includes some of the mesic upland woodlands represented by the significant indicator trees *Juglans californica* and *Umbellularia californica*. The vine *Marah macrocarpus* is also an indicator of this group, which is closely related to the following group.

Group 42 represents the coastal woodlands in all stages from recently disturbed to mature. Thus, along with the two main oak tree species, shrubs and herbs associated with the understories or seral openings of these woodlands are also among the principle indicators. The most significant indicators in order of importance value are: *Quercus agrifolia*, *Toxicodendron diversilobum*, *Mimulus aurantiacus*, *Platanus racemosa*, *Rhamnus ilicifolia*, *Sambucus mexicana*, *Dryopteris arguta*, *Quercus lobata*, *Keckiella cordifolia*, *Bromus carinatus*, *Carduus pycnocephalus*, *Rubus ursinus*, and *Venegasia carpesioides*. It is interesting to note that *Platanus racemosa* sorts out here, suggesting a closer relationship to oak woodlands than to the strictly riparian vegetation including *Salix* spp., *Alnus rhombifolia*, and others found in Group 1.

Vegetation Types

We present here a listing of the vegetation types defined for the Santa Monica Mountains and environs. These are the result of naming the finer branches of the main cluster groups described above using the methods defined. Alliances and associations (with their phases) that are marked by an asterisk (*) are fully described in the report *Vegetation classification of the Santa Monica Mountains National Recreation Area and environs in Ventura and Los Angeles Counties, California* (Keeler-Wolf and Evens 2006). An electronic copy of this report may be obtained free of charge (see Literature Cited for details). Full descriptions of alliances not described in this report may be found in the second edition of the *Manual of California Vegetation* (Sawyer et al. 2007).

Definitions

Alliance: The generic unit of vegetation classification in the National Vegetation Classification system. An alliance is defined usually by the dominant and characteristic plant species in the layer of vegetation with the highest cover. For example, in the California Sycamore alliance, California sycamore is conspicuous or dominant in the tree canopy (with canopy • 10% absolute cover). However, it may occur along with other tree species such as oaks and willows, and with numerous other shrub and herb species. Those other species typically cover less ground and/or are less characteristic of the alliance than is the sycamore.

Association: The fundamental unit of classification in the National Vegetation Classification system. This is analogous to the species in organismal taxonomy. Associations tend to be localized to a particular geographic subregion (such as a certain mountain range) and are clearly associated with a certain environmental setting. Associations are built up into the larger units of alliances based on constant patterns of subordinate species within an overall pattern of constant species dominance. For example, although the California Sagebrush Alliance is widespread in coastal central and southern California, the California Sagebrush-Ashy Buckwheat Association is only found in the Santa Monica Mountains.

Phase: An informal unit of classification accommodating local floristic variation that tends not to have obvious correlations with particular environmental conditions. It probably results from particularly localized environmental conditions, site history, or fire history.

Symbols: A dash (-) is used in a classification unit to define more than one species in the same layer of vegetation. A slash (/) is used in a classification unit to separate species that are found in more than one layer of vegetation. Thus, the *Platanus racemosa-Quercus agrifolia/Baccharis salicifolia/Artemisia douglasiana* Association is defined by two trees, one shrub, and an herb.

TREE OVERSTORY VEGETATION

Alnus rhombifolia Woodland/Forest Alliance
    Alnus rhombifolia-Platanus racemosa Woodland/Forest Association*
Eucalyptus Woodland/Forest Alliance*
Juglans californica Woodland/Forest Alliance
    Juglans californica/Annual Grass-Herb Woodland/Forest Association*
    Juglans californica/Artemisia californica/Leymus condensatus Woodland/Forest
    Association*
    Juglans californica/Ceanothus spinosus Woodland/Forest Association*
    Juglans californica/Heteromeles arbutifolia Woodland/Forest Association*
    Juglans californica/Malosma laurina Woodland/Forest Association*
Platanus racemosa Woodland/Forest Alliance
    Platanus racemosa South Coast Intermittent Stream Woodland/Forest Association*
    Platanus racemosa/Annual Grass-Herb Woodland/Forest Association*
    Platanus racemosa-Quercus agrifolia South Coast Woodland/Forest Association*
    *Platanus racemosa-Quercus agrifolia/Baccharis salicifolia/Artemisia douglasiana South
    Coast* Woodland/Forest Association*
    Platanus racemosa-Quercus agrifolia-Salix lasiolepis Woodland/Forest Association*
Quercus agrifolia Woodland/Forest Alliance
    Quercus agrifolia South Coastal Woodland/Forest Association*
    Quercus agrifolia/Adenostoma fasciculatum Woodland/Forest Association*
    Quercus agrifolia/Annual Grass-Herb Woodland/Forest Association*
    Quercus agrifolia/Ceanothus spinosus Woodland/Forest Association*
    Quercus agrifolia/Heteromeles arbutifolia Woodland/Forest Association*
        Quercus agrifolia/Heteromeles arbutifolia Phase
        Quercus agrifolia/Malosma laurina Phase
    Quercus agrifolia/Quercus berberidifolia Woodland/Forest Association*
    Quercus agrifolia/Salvia leucophylla-Artemisia californica Woodland/Forest Association*
    Quercus agrifolia/Toxicodendron diversilobum Woodland/Forest Association*
        Quercus agrifolia/Toxicodendron diversilobum Phase
        Quercus agrifolia/Mimulus aurantiacus Phase
    Quercus agrifolia-Juglans californica Woodland/Forest Association*
        Quercus agrifolia-Juglans californica Phase
        Quercus agrifolia-Juglans californica /Toxicodendron diversilobum Phase
    Quercus agrifolia-Salix lasiolepis Woodland/Forest Association*
    Quercus agrifolia-Umbellularia californica Woodland/Forest Association*
        Quercus agrifolia-Umbellularia californica Phase
        Quercus agrifolia-Umbellularia californica/Toxicodendron diversilobum Phase
    Quercus agrifolia-Umbellularia californica/Ceanothus oliganthus Woodland/Forest
    Association*

Quercus lobata Woodland Forest Alliance
> *Quercus lobata*/Annual Grass-Herb Woodland/Forest Association*
> *Quercus lobata-Quercus agrifolia*/Annual Grass-Herb Woodland/Forest Association*
> *Quercus lobata-Salix lasiolepis* Woodland/Forest Association*

Salix laevigata Woodland Forest Alliance
> **Salix laevigata-Salix lasiolepis Woodland/Forest Sub-Alliance***
>> *Salix laevigata-Salix lasiolepis/Artemisia douglasiana-Rubus ursinus*/Annual Grass-Herb Woodland/Forest Association*
>> *Salix laevigata-Salix lasiolepis/Baccharis salicifolia* Woodland/Forest Association*

Salix lasiolepis Woodland/Forest Alliance*
> *Salix lasiolepis/Baccharis salicifolia* Woodland/Forest Association*
> *Salix lasiolepis/Malosma laurina* Woodland/Forest Association*

Schinus molle Woodland/Forest Alliance*

Umbellularia californica Woodland/Forest Alliance
> *Umbellularia californica/Ceanothus oliganthus* Woodland/Forest Association*
> *Umbellularia californica-Alnus rhombifolia* Woodland/Forest (provisional) Association*
> *Umbellularia californica-Juglans californica/Ceanothus spinosus* Woodland/Forest Association*
> *Umbellularia californica-Platanus racemosa* Woodland/Forest Association*

SHRUB OVERSTORY VEGETATION

Adenostoma fasciculatum Shrubland Alliance
> *Adenostoma fasciculatum* Shrubland Association*
> *Adenostoma fasciculatum-Ceanothus megacarpus* Shrubland Association*
> *Adenostoma fasciculatum-Eriogonum fasciculatum* Shrubland Association*
>> *Adenostoma fasciculatum-Eriogonum fasciculatum* /Annual Grass-Herb Phase
>> *Adenostoma fasciculatum-Lotus scoparius-Dendromecon rigida* Phase
> *Adenostoma fasciculatum-Malosma laurina* Shrubland Association*
> *Adenostoma fasciculatum-Malosma laurina-Eriodictyon crassifolium*/Annual Grass-Herb Shrubland Association*
> *Adenostoma fasciculatum-Mimulus aurantiacus* Shrubland Association*
> *Adenostoma fasciculatum-Salvia leucophylla* Shrubland Association*

Adenostoma fasciculatum-Adenostoma sparsifolium Shrubland Alliance
> *Adenostoma fasciculatum-Adenostoma sparsifolium-Ceanothus crassifolius* Shrubland Association*

Adenostoma fasciculatum-Arctostaphylos glandulosa Shrubland Alliance
> *Adenostoma fasciculatum-Arctostaphylos glandulosa* Shrubland Association*
>> *Adenostoma fasciculatum-Arctostaphylos glandulosa* Phase
>> *Adenostoma fasciculatum-Ceanothus megacarpus-Arctostaphylos glandulosa* Phase

Adenostoma fasciculatum-Arctostaphylos glauca Shrubland Alliance
> *Adenostoma fasciculatum-Arctostaphylos glauca* Shrubland Association*

Adenostoma fasciculatum-Ceanothus crassifolius Shrubland Alliance
> *Adenostoma fasciculatum-Ceanothus crassifolius-Malosma laurina* Shrubland Association*

Adenostoma fasciculatum-Ceanothus cuneatus Shrubland Alliance
> *Adenostoma fasciculatum-Ceanothus cuneatus-Salvia mellifera-Malosma laurina* Shrubland Association*

Adenostoma fasciculatum-Salvia mellifera Shrubland Alliance
> *Adenostoma fasciculatum-Salvia mellifera* Shrubland Association*
> *Adenostoma fasciculatum-Salvia mellifera-Malosma laurina* Shrubland Association*

Adenostoma fasciculatum-Salvia mellifera-Rhus ovata Shrubland Association*
Adenostoma sparsifolium Shrubland Alliance*
Arctostaphylos glandulosa Shrubland Alliance*
Arctostaphylos glauca Shrubland Alliance*
Artemisia californica Shrubland Alliance
    Artemisia californica Shrubland Association*
        Artemisia californica/Annual Grass-Herb Phase
        Artemisia californica-Malosma laurina Phase
        Artemisia californica-Salvia leucophylla Phase
    Artemisia californica/Leymus condensatus Shrubland Association*
    Artemisia californica-Eriogonum cinereum Shrubland Association*
        Artemisia californica-Eriogonum cinereum Phase
        Artemisia californica-Eriogonum cinereum-Mimulus aurantiacus/Melica imperfecta Phase
    Artemisia californica-Mimulus aurantiacus Shrubland Association*
Artemisia californica-Eriogonum fasciculatum Shrubland Alliance
    Artemisia californica-Eriogonum fasciculatum/Annual Grass-Herb Shrubland Association*
    Artemisia californica-Eriogonum fasciculatum-Salvia leucophylla Shrubland Association*
    Artemisia californica-Eriogonum fasciculatum-Salvia mellifera Shrubland Association*
Atriplex lentiformis Shrubland Alliance*
Baccharis pilularis Shrubland Alliance
    Baccharis pilularis/Annual Grass-Herb Shrubland Association*
    Baccharis pilularis-Artemisia californica Shrubland Association*
        Baccharis pilularis-Artemisia californica Phase
        Baccharis pilularis-Artemisia californica-Salvia leucophylla Phase
        Baccharis pilularis-Malosma laurina-Artemisia californica Phase
Baccharis salicifolia Shrubland Alliance
    Baccharis salicifolia Riparian Shrubland Association*
Ceanothus crassifolius Shrubland Alliance
    Ceanothus crassifolius Shrubland Association*
    Ceanothus crassifolius-Malosma laurina Shrubland Association*
Ceanothus cuneatus Shrubland Alliance
    Ceanothus cuneatus-Quercus berberidifolia Shrubland Association*
Ceanothus megacarpus Shrubland Alliance
    Ceanothus megacarpus Shrubland Association*
    Ceanothus megacarpus-Adenostoma fasciculatum Shrubland Association*
        Ceanothus megacarpus-Adenostoma fasciculatum Phase
        Ceanothus megacarpus-Adenostoma fasciculatum-Salvia mellifera Phase
    Ceanothus megacarpus-Adenostoma sparsifolium Shrubland Association*
    Ceanothus megacarpus-Cercocarpus betuloides Shrubland Association*
    Ceanothus megacarpus-Malosma laurina Shrubland Association*
        Ceanothus megacarpus-Malosma laurina Phase
        Ceanothus megacarpus-Malosma laurina-Adensotoma fasciculatum Phase
    Ceanothus megacarpus-Salvia mellifera Shrubland Association*
Ceanothus oliganthus Shrubland Alliance
    Ceanothus oliganthus Shrubland Association*
    Ceanothus oliganthus-Adenostoma sparsifolium Shrubland Association*
    Ceanothus oliganthus-Heteromeles arbutifolia-Rhus ovata Shrubland Association*
    Ceanothus oliganthus-Quercus berberidifolia Shrubland Association*
Ceanothus spinosus Shrubland Alliance
    Ceanothus spinosus Shrubland Association*

Ceanothus spinosus Phase
Ceanothus spinosus-Malosma laurina Phase
Ceanothus spinosus-Heteromeles arbutifolia-Prunus ilicifolia Phase
Ceanothus spinosus-Ceanothus megacarpus Shrubland Association*
Cercocarpus betuloides Shrubland Alliance
Cercocarpus betuloides Shrubland Association*
Cercocarpus betuloides-Adenostoma fasciculatum Shrubland Association*
Cercocarpus betuloides-Ceanothus spinosus Shrubland Association *
Cercocarpus betuloides-Malosma laurina-Artemisia californica Shrubland Association*
Cercocarpus betuloides-Malosma laurina-Artemisia californica Phase
Cercocarpus betuloides-Artemisia californica/Melica imperfecta Phase
Coreopsis gigantea Shrubland Alliance
Coreopsis gigantea-Artemisia californica-Eriogonum cinereum Shrubland Association*
Coreopsis gigantea-Ericameria ericoides-Encelia californica Shrubland Association*
Dendromecon rigida Shrubland Alliance*
Encelia californica Shrubland Alliance
Encelia californica Shrubland Association*
Encelia californica Phase
Encelia californica-Eriogonum fasciculatum Phase
Encelia californica-Artemisia californica Shrubland Association*
Encelia californica-Eriogonum cinereum Shrubland Association*
Encelia californica-Malosma laurina-Salvia mellifera Shrubland Association*
Encelia californica-Rhus integrifolia Shrubland Association*
Eriogonum cinereum Shrubland Alliance
Eriogonum cinereum Shrubland Association*
*Eriogonum cinereum/*Annual Grass-Herb Phase
Eriogonum cinereum-Malacothamnus fasciculatus/Leymus condensatus Phase
Eriogonum fasciculatum Shrubland Alliance
Eriogonum fasciculatum Shrubland Association*
Eriogonum fasciculatum Phase
Eriogonum fasciculatum-Lotus scoparius Phase
Eriogonum fasciculatum-Salvia mellifera-Malosma laurina Shrubland Association*
Eriogonum fasciculatum-Salvia apiana Shrubland Alliance*
Hazardia squarrosa Shrubland Alliance
Hazardia squarrosa/Nassella pulchra-Hemizonia fasciculata Shrubland Association*
Hazardia squarrosa-Artemisia californica Shrubland Association*
*Hazardia squarrosa/*Annual Grass-Herb
Hazardia squarrosa-Artemisia californica/Leymus condensatus
Heteromeles arbutifolia Shrubland Alliance
Heteromeles arbutifolia-Malosma laurina Shrubland Association*
Heteromeles arbutifolia-Malosma laurina Phase
Heteromeles arbutifolia Phase
Heteromeles arbutifolia-Cercocarpus betuloides Phase
Heteromeles arbutifolia-Salvia mellifera Phase
Heteromeles arbutifolia-Artemisia californica-Mimulus aurantiacus Phase
Lepidospartum squamatum Shrubland Alliance*
Lotus scoparius Shrubland Alliance
Lotus scoparius Shrubland Association*
*Lotus scoparius-Artemisia californica/*Annual Grass-Herb Phase
Lotus scoparius-Malacothamnus fasciculatus-Adenostoma fasciculatum-Salvia mellifera Phase

***Malacothamnus fasciculatus* Shrubland Alliance**
    Malacothamnus fasciculatus Shrubland Association*
    Malacothamnus fasciculatus-Ceanothus megacarpus Shrubland Association*
    Malacothamnus fasciculatus-Ceanothus spinosus Shrubland Association*
    Malacothamnus fasciculatus-Malosma laurina Shrubland Association*
    Malacothamnus fasciculatus-Salvia leucophylla Shrubland Association*
    Malacothamnus fasciculatus-Salvia mellifera Shrubland Association*

***Malosma laurina* Shrubland Alliance**
    Malosma laurina Shrubland Association*
        Malosma laurina Phase
        Malosma laurina/Annual Grass-Herb Phase
    Malosma laurina-Artemisia californica Shrubland Association*
        Malosma laurina-Artemisia californica Phase
        Malosma laurina-Artemisia californica-Salvia leucophylla Phase
    Malosma laurina-Eriogonum cinereum Shrubland Association*
        Malosma laurina-Eriogonum cinereum Phase
        Malosma laurina-Eriogonum cinereum-Lotus scoparius Phase
        Malosma laurina-Eriogonum cinereum-Salvia mellifera Phase
        Malosma laurina-Malacothamnus fasciculatus-Eriogonum cinereum-Salvia mellifera Phase
        Malosma laurina-Rhus integrifolia-Eriogonum cinereum-Artemisia californica Phase
    Malosma laurina-Eriogonum fasciculatum Shrubland Association*
        Malosma laurina-Eriogonum fasciculatum Phase
        Malosma laurina-Eriogonum fasciculatum-Artemisia californica/Annual Grass-Herb Phase
        Malosma laurina-Eriogonum fasciculatum-Heteromeles arbutifolia-Ceanothus megacarpus Phase
    Malosma laurina-Rhus ovata-Ceanothus megacarpus Shrubland Association*
    Malosma laurina-Salvia mellifera Shrubland Association*

Mesembryanthemum* spp.-*Carpobrotus* spp. *Semi-natural* Shrubland Alliance
***Mimulus aurantiacus* Shrubland Alliance**
    Mimulus aurantiacus Shrubland Association*
        Mimulus aurantiacus-Malosma laurina Phase
        Mimulus aurantiacus-Salvia leucophylla Phase

***Opuntia* spp. Shrubland Alliance**
    Opuntia spp.-*Mixed Coastal Sage Scrub* Shrubland Association*

***Prunus ilicifolia* Shrubland Alliance**
    Prunus ilicifolia-Heteromeles arbutifolia Shrubland Association*

***Quercus berberidifolia* Shrubland Alliance**
    Quercus berberidifolia Shrubland Association*
        Quercus berberidifolia Phase
        Quercus berberidifolia-Adenostoma fasciculatum Phase
        Quercus berberidifolia-Heteromeles arbutifolia Phase
    Quercus berberidifolia-Ceanothus spinosus Shrubland Association*

***Quercus berberidifolia-Adenostoma fasciculatum* Shrubland Alliance**
    Quercus berberidifolia-Adenostoma fasciculatum Shrubland Association*

***Quercus berberidifolia-Cercocarpus betuloides* Shrubland Alliance**
    Quercus berberidifolia-Cercocarpus betuloides Shrubland Association*

Quercus wislizeni* var. *frutescens* Shrubland Alliance
Rosa californica* Shrubland Alliance
***Rhus integrifolia* Shrubland Alliance**

Rhus integrifolia Shrubland Association*
    Rhus integrifolia Phase
    Rhus integrifolia-Heteromeles arbutifolia Phase
    Rhus integrifolia-Malacothamnus fasciculatus Phase
Rhus integrifolia-Artemisia californica-Eriogonum cinereum Shrubland Association*
    Rhus integrifolia-Artemisia californica-Salvia leucophylla Phase
    Rhus integrifolia-Eriogonum cinereum-Yucca whipplei-Coreopsis gigantea Phase
Rhus integrifolia-Opuntia spp.-*Eriogonum cinereum* Shrubland Association*
Rhus ovata Shrubland Alliance
    Rhus ovata Shrubland Association*
    Rhus ovata-Salvia leucophylla-Artemisia californica Shrubland Association*
Salix exigua Shrubland Alliance*
Salvia leucophylla Shrubland Alliance
    Salvia leucophylla Shrubland Association*
        Salvia leucophylla-Artemisia californica Phase
        Salvia leucophylla- Artemisia californica-Malacothamnus fasciculatus Phase
        Salvia leucophylla/Leymus condensatus Phase
        Salvia leucophylla/Nassella spp. Phase
    Salvia leucophylla- Artemisia californica Shrubland Association*
        Salvia leucophylla- Artemisia californica Phase
        Salvia leucophylla- Artemisia californica/Leymus condensatus Phase
    Salvia leucophylla-Artemisia californica-Eriogonum cinereum/Nassella spp. Shrubland Association*
        Salvia leucophylla-Artemisia californica-Eriogonum cinereum/Nassella spp. Phase
        Salvia leucophylla-Artemisia californica-Malosma laurina/Nassella spp. Phase
        Salvia leucophylla-Artemisia californica-Mimulus aurantiacus Phase
    Salvia leucophylla-Eriogonum cinereum/Annual Grass-Herb Shrubland Association*
Salvia mellifera Shrubland Alliance
    Salvia mellifera Shrubland Association*
        Salvia mellifera Phase
        Salvia mellifera-Adenostoma fasciculatum Phase
        Salvia mellifera-Eriogonum fasciculatum Phase
        Salvia mellifera- Malacothamnus fasciculatus Phase
    Salvia mellifera-Eriogonum cinereum Shrubland Association*
    Salvia mellifera-Malosma laurina Shrubland Association*
        Salvia mellifera-Malosma laurina Phase
        Salvia mellifera-Artemisia californica-Rhus integrifolia Phase
    Salvia mellifera-Rhus ovata Shrubland Association*
    Salvia mellifera-Artemisia californica Shrubland Association*
Sambucus mexicana Shrubland Alliance
    Sambucus mexicana/Leymus condensatus-Annual Herb Shrubland Association*
    Sambucus mexicana-Heteromeles arbutifolia/Annual Grass-Herb Shrubland Association*
Spartium junceum Shrubland Alliance*
Toxicodendron diversilobum Shrubland Alliance
    Toxicodendron diversilobum-Artemisia californica/Leymus condensatus Shrubland Association*
    Toxicodendron diversilobum-Mimulus aurantiacus Shrubland Association*
Venegasia carpesioides Shrubland Alliance*

HERBACEOUS VEGETATION

Arundo donax Herbaceous Alliance*
Avena spp. Herbaceous Alliance
  Avena fatua Herbaceous Association*
California Annual Grassland/Herbaceous Alliance*
  Brassica nigra Herbaceous Association*
  Brassica nigra-Bromus diandrus Herbaceous Association*
  Brassica nigra-Centaurea melitensis Herbaceous Association*
  Bromus diandrus Herbaceous Association*
  Bromus diandrus-Avena spp. Herbaceous Association*
Distichlis spicata Herbaceous Alliance
  Distichlis spicata-Ambrosia chamissonis Herbaceous Association*
  Distichlis spicata-Salicornia virginica-Jaumea carnosa Herbaceous Association*
    Distichlis spicata-Salicornia virginica-Jaumea carnosa Phase
    Distichlis spicata-Jaumea carnosa Phase
Euphorbia terracina Herbaceous Stands*
Foeniculum vulgare Herbaceous Alliance*
Frankenia salina Herbaceous Alliance*
  Frankenia salina-Limonium californicum-Monanthochloe littoralis-Salicornia spp.
  Herbaceous Association*
Juncus effusus Herbaceous Alliance*
Lepidium latifolium Herbaceous Alliance
  Lepidium latifolium Herbaceous Association*
Leymus condensatus Herbaceous Alliance
  Leymus condensatus Herbaceous Association*
Leymus triticoides Herbaceous Alliance*
Lolium multiflorum Herbaceous Alliance
  Lolium multiflorum Herbaceous Association*
Nassella lepida Herbaceous Alliance*
Nassella pulchra Herbaceous Alliance*
  Nassella pulchra-Hazardia squarrosa Herbaceous Association*
Pennisetum setaceum Herbaceous Alliance*
  Pennisetum setaceum-Coreopsis gigantea-Yucca whipplei-Malosma laurina Herbaceous
  Association*
Phalaris aquatica Herbaceous Alliance*
Salicornia virginica Herbaceous Alliance*
  Salicornia virginica/Algae Herbaceous Association*
  Salicornia virginica-Brassica nigra Herbaceous Association*
  Salicornia virginica-Frankenia salina-Suaeda taxifolia (synonym *Suaeda californica* var.
  taxifolia) Herbaceous Association*
    Salicornia virginica-Frankenia salina-Suaeda taxifolia Phase
    Salicornia virginica-Frankenia salina-Batis maritime Phase
    Salicornia virginica-Suaeda taxifolia Phase
  Salicornia virginica-Salicornia subterminalis Herbaceous Association*
Scirpus acutus-Scirpus californicus Herbaceous Alliance*
Selaginella bigelovii Herbaceous Alliance
  Selaginella bigelovii/Eriogonum fasciculatum Association*
Typha spp. Herbaceous Alliance*

DISCUSSION

Overview of the Santa Monica Mountains Vegetation Patterns

In reviewing the 10 major vegetation groups described above, a general portrait of the current vegetation conditions of the area is unveiled. Since the sample allocation is representative of the array of all vegetation conditions throughout the area, these main groupings show the organizing principles of the vegetation of the region. Significant among them are the importance of both the strong temperature and moisture gradients, indicated by groups restricted to either largely maritime (groups 4, 12, and 16) or upland-continental (group 33) settings, or hot and dry (groups 16, 24, 33) versus moist and shady conditions (groups 4, 41, and 42). Groups defined primarily by recent disturbance or early seral conditions (groups 1, 16, and 55) are also prominent. The close ecological relationship of mesic (north-slope) chaparral and woodlands characterized by oaks and other species is also shown in the cluster groupings. The California walnut and bay woodlands are more similar to mesic chaparral than they are to the coast live oak woodlands.

The overwhelming presence of upland settings within the Santa Monica Mountains area is suggested by the inclusion of most major wetland vegetation (including salt marsh and fresh water types) within a larger group of herbaceous and early seral species at this basic level of differentiation. This is unlike many other regional vegetation classification analyses, where wetland types tend to split very early from other upland types. The complete integration of many non-native species into the list of indicator species for several of these groups underscores the reality that these species are now deeply imbedded members of the local flora and ecology of the region.

Philosophy of Vegetation Classification Used in this Analysis

The developing philosophy of vegetation classification in California has benefited from a large number of recent classification projects centered in southern coastal California (DeSimone and Burk 1992, Gordon and White 1994, White and Padley 1997, Borchert et al. 2004, Evens and San 2005, Klein and Evens 2005). These, in conjunction with a growing understanding of statewide vegetation, have enabled the classification of the vegetation in the current project to proceed within a broader and better framework than would have been possible as little as five years ago. The natural development of most taxonomies, whether they be of species or vegetation, work their way through what can be called an expansive phase and then a synthetic phase. The first is characterized by the proliferation of many taxa based on local description without the benefit of broad comparison of related types. The second is based on a retrospective and broader view of more studies where related taxa can be compared and often shown to be related, thus ultimately synonymized. This latter phase has begun to take place in much of California, especially with the preparation of the second edition of *A Manual of California Vegetation* (Sawyer et al. 2007).

For example, chaparral alliances defined in previous studies included several mixed species types including the *Eriogonum fasciculatum-Encelia farinosa* type (Gordon and White 1994), *Ceanothus megacarpus-Cercocarpus betuloides,* and *Ceanothus megacarpus-Rhamnus ilicifolia* types (Borchert et al. 2004). These were named by the characteristic co-dominance of shrub species and were thought initially to represent fundamentally different entities than stands of vegetation dominated singly by individual species, for example, *Encelia farinosa* (without significant cover of *Eriogonum fasciculatum*) or *Ceanothus megacarpus* (without significant cover of *Cercocarpus betuloides*). However, now with a broader regional perspective, it is becoming clear that these entities are really more generally defined by the presence of a single characteristic species that may or may not have shared dominance with a less characteristic

species. In the above examples, the *Eriogonum. fasciculatum-Encelia farinosa* type has been subsumed under the *Encelia farinosa* alliance, while the *Ceanothus megacarpus-Cercocarpus betuloides* alliance and the *Ceanothus megacarpus-Rhamnus ilicifolia* alliance have been subsumed under the *Ceanothus megacarpus* alliance.

There are various lines of reasoning used to make these decisions. However, central to most of them is a broader understanding of both the geographic distribution and internal variation of each association defined within these alliances. A mixed alliance should have a broad regional distribution of the co-dominant species with further sub-regional variations of the associations to be substantiated as a co-dominant alliance. One example of this is the *Artemisia californica–Eriogonum fasciculatum* Alliance, which occurs from San Diego County and northwestern Baja California, north to the Diablo Range of Alameda County.

One of the great benefits of collecting so many samples of vegetation stands in this current project is that we can now see a more complete approximation of the range in cover of species and environmental conditions for each alliance and association. We have a better sense of where the important "breaks" in species composition are in these patterns. We can also compare vegetation samples from similar areas away from the Santa Monica Mountains and determine if the characteristics are indeed different or similar. Using these kinds of comparisons for many parts of southern California, we have begun to synthesize some of the complicated patterns described in earlier quantitative efforts and, in some cases, simplify them.

For example, although *Salvia leucophylla* forms stands where it is the only dominant as well as mixed stands with *Artemisia californica* in the Santa Monica Mountains, we now believe that both of these situations can be encapsulated within the *Salvia leucophylla* Alliance, rather than establishing a separate alliance for the single dominant and co-dominant situations. This is a result of *Salvia leucophylla* being relatively geographically restricted, whereby it only dominates in the "Venturan" coastal scrub zone between Santa Barbara and Orange counties (Westman 1981, Malanson 1984). When *S. leucophylla* makes up an important component of the shrub cover, whether it is the dominant species or is co-dominant with another species, it is sufficient to define the alliance (Figure 7). On the other hand, a mixed alliance with *Artemisia californica and Salvia mellifera* has a much broader distribution up and down the California Coast Ranges and into Baja California. It occurs under different ecological conditions than either of the single species alliances dominated by *Salvia mellifera* or *Artemisia californica*. For example, in the Central Coast Ranges, there is an association of *A. californica and S. mellifera* defined by co-dominance of the two shrubs (Evens and San 2004). This same association is also defined for western Riverside (Klein and Evens 2005) and Orange counties (DeSimone and Burke 1992). The wide-ranging consistency of this vegetation is a strong factor in maintaining it as a separate entity from either the *Artemisia californica* or the *Salvia mellifera* Alliance.

The philosophy of this classification is consistent with other classifications produced for national parks in California. We require a relatively large number of samples to set high confidence for the existence of an association. In general, we have accepted n = 10 or more as a threshold for high confidence. Any less would set lower confidence, unless the same characteristics of species composition and environmental variables have been previously well defined in studies elsewhere.

Further revisions are bound to occur in the California state classification as more data are analyzed and compared. As a result of relatively rigorous definitions at the association level, it is likely that these modifications will be made at the alliance level as well. The associations that are defined currently in this classification are well substantiated by large sample sizes with consistent species compositions and relative cover values. The separation of associations into different

Figure 7. *Salvia leucophylla* (Purple Sage) Alliance with the nominate species as a dominant or co-dominant shrub.

alliances would only be reasonable if we found major environmental differences in these alliances. Further revisions could also occur as datasets from different regions are analyzed together to identify and differentiate major environmental patterns of the alliances. One further refinement of the classification rules realized in this project was the treatment of large "emergent" shrubs. In earlier efforts in the California deserts and desert transition areas (Keeler-Wolf et al. 1998, Thomas et al. 2004), tall shrubs or "dwarf trees," such as *Juniperus californica, Rhus ovata, Cercidium florida, Olneya tesota*, and others were emphasized in numerical classification when they occurred in association with shorter-stature drought-deciduous desert and semi-desert shrubs such as *Encelia farinosa, Salvia apiana, Viguiera parishii*, and *Eriogonum fasciculatum*. Thus, despite a possible higher overall cover of individuals of the shorter drought-deciduous species, the larger, evenly spaced emergent species were found to "drive" the classification by their presence rather than by their total percent cover in a stand. This meant alliances and associations were often named by the larger, less dense emergent species.

Structurally similar situations exist in the Santa Monica Mountains where *Rhus ovata* and especially *Malosma laurina* occur at relatively low density and cover over a shorter, but higher cover layer of drought-deciduous shrubs such as *Artemisia californica, Encelia californica, Eriogonum cinereum, E. fasciculatum, Salvia mellifera*, and *S. leucophylla*. The initial classification developed for the Santa Monica Mountains before extensive data analysis stressed

the presence of such species as *Malosma laurina*, even if they had a much lower cover than the associated shorter drought-deciduous shrubs.

This structural relationship was not borne out in the first phase of data analysis. Instead, it became clear that the presence of shrubs such as *Malosma laurina* was often ubiquitous, occurring in many situations that were better defined in many cases by the associated shorter-stature drought-deciduous shrubs. The concept of the *M. laurina* Alliance was refined to include only those stands where *M. laurina* was dominant or co-dominant with other shrubs (regardless of their stature) in the stand (Figure 8). This is one of many cautionary tales revolving around vegetation classification assumptions based on extrapolating data from seemingly similar situations in different geographies and environments.

Figure 8. *Malosma laurina* (Laurel Sumac) Alliance is recognized when the species is dominant or strongly co-dominant with other coastal sage scrub species.

CONCLUSIONS AND LESSONS LEARNED FROM THIS APPROACH

The Santa Monica Mountains vegetation project has been the most data-intensive mapping effort to date for any U.S. National Park Service vegetation inventory. Most samples were Vegetation

Rapid Assessments (RAs). To conclude, we briefly touch upon four major points relating to the techniques used in this project:

1) How well did rapid assessments capture the diversity of the vegetation in the park?
2) Did the large sample size help or hinder the classification effort?
3) Did the large sample size help or hinder the mapping and monitoring effort?
4) Did sampling throughout the year hinder analysis and interpretation of the results due to phonological variation?

Capturing the diversity of vegetation

Some vegetation types were underrepresented in the sampling effort. The full spectrum of vegetation in the area was not surveyed because the study area had mixed ownership and accessibility. For these reasons, adequate data may not be available for all vegetation types. However, samples representing unusual species groupings in the study area are considered important, and worthy of additional sampling. These types are classified at a more generic alliance/habitat level or as unique stands.

Large numbers of samples were allocated both by the parameters of the GRADSECT analysis and by the on-the-ground analysis of field crew leaders and photo-interpreters when we encountered new and unusual vegetation. In general, the coordination of rapid assessment and relevé sampling was successful and the concordance in the classification between rapid assessments (where a partial list of up to 20 major species were listed within the stand assessed) and relevés (where full species data were collected in a plot) was high. Several other sampling projects (e.g., Borchert et al 2004, Gordon and White 1994, Thomas et al 2004) have confirmed that sampling woody chaparral and scrub in southern California is not driven strongly by herbaceous species in the understory. Thus, for rapid assessments, the reduced emphasis on inventorying the full component of the shrubland understory in favor of the woody species in the overstory did not appear to affect the results of the classification.

In addition, samples were conducted using relevés for vegetation types with particularly high species diversity and with notable herbaceous components. Capturing the variety of herb-dominated vegetation in the park was less critical to fire managers, and it understandably has been a much more difficult task due to the strong inter- and intra-seasonal variation in vegetation mainly characterized by annual species. This latter issue remains a problem with all types of vegetation sampling currently conducted in California.

Large sample size and classification

The exceptionally robust data set, collected in a standard way by the same crew of botanists within a two-year period, increased the reliability of the data. In contrast to many earlier park efforts, where retrospective data were combined with a small dataset of newly collected information for a classification, this current approach was preferable. No complaints have arisen about the quality of the data because the high sample sizes are enviable in most cases. The plant associations were defined by an average of about 20 samples, substantially higher than the average for any other parks assessed in California. However, the large data set lead to more detailed analysis due to the predilection for more samples to be more finely divided through clustering techniques.

We still believe that this project tended to over-divide some types despite the rational and tempered approach we used in the classification, based on comparison in scale and resolution of

plant associations defined in other parts of southern California. This over-division was noticed in addition to the informally defined phases, which are clearly minor subdivisions of associations. Part of the issue in this park's process revolved around collecting multiple samples of all successional phases of vegetation, and so many of the definitions describe seral stages of vegetation that could perhaps be more broadly defined. This approach was clearly advantageous to the park managers, as they needed to obtain information on the post-fire stages for mapping purposes. However, it may be more detailed than other national vegetation classification standards. In the full report, comments are made on which associations are best defined floristically and which ones may be more minor variants of other broader types.

One certainty was that the huge amount of data collected required substantially more time for analysis and description than was predicted. This would not have been possible without thorough collaboration between park staff and contractors in data collection, analysis, and description phases of the project. Without innovative approaches such as the development of queries of the database and automation of the report writing process, this project would have gone much more over budget than it did. We recommend that the projected amount of analysis and description time could be essentially doubled for future projects where such detail is required.

Large samples for monitoring and modeling

All collaborators on the project have agreed that the variety and numbers of samples collected generally strengthened the utility of this project for the classification and map accuracy. The robust data set also increased the potential for a variety of field-based monitoring and modeling projects, both structural and floristic. Despite the temporary nature of the samples, Global Positioning Systems technology with accurate and complete location information will enable the re-location of most samples for time sequence analysis.

Year-round sampling

One final question was whether the decision to sample vegetation in chaparral and coastal scrub vegetation throughout the year had any major influence on the results of the classification. Certainly because there were drought- or seasonally-deciduous species of *Salvia*, *Eriogonum*, *Artemisia*, and others in coastal scrub, sampling the same stand in April versus August likely yielded much higher cover of these species. Likewise, sampling a stand of *Juglans californica* in December versus June yielded much lower cover of that winter deciduous tree. Our range of cover estimates for these deciduous species was higher than if we standardized data collection during peak phenology. However, this required us to put broader requirements of membership on many of the vegetation types, a characteristic which tempered proliferation of vegetation types based on range of cover alone. We have not noticed a general trend in the data to average somewhat lower cover estimates for many of these deciduous species, compared to other studies. Thus, again the large sample size (many of which were collected in high phenology periods) appeared to ameliorate the range of variance. The value of year-round sampling increased substantially the efficiency of the crews and also logistically enabled the same personnel to remain on the project throughout the duration, vastly improving the consistency and reliability of the data collected through the project.

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FREEZING TOLERANCE IMPACTS CHAPARRAL SPECIES DISTRIBUTION IN THE SANTA MONICA MOUNTAINS

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ABSTRACT: A shift in chaparral species composition occurs from coastal to inland sites of the Santa Monica Mountains of southern California. Past studies have attributed this pattern to differential adaptations of chaparral species to gradients in moisture and solar radiation. We examined an alternate hypothesis, that shifts in species composition from coastal to inland sites is a result of differential response to freezing and the interactions of freezing with drought. Coastal sites rarely experience air temperatures below 0 °C whereas just 5 to 6 km inland, cold valleys experience temperatures as low as -12 °C. Seasonal drought can last 6 to 8 months and may extend, on rare occasions, into the month of December, coincidental with the onset of winter freeze. Either water stress or freezing, by independent mechanisms, can induce embolism in stem xylem and block water transport from soil to leaves, leading to branchlet dieback or whole shoot death. Water stress in combination with freezing may enhance xylem embolism formation. Post-fire seedlings are especially vulnerable because of greater tissue sensitivity to freezing injury, diminutive roots that preclude access to deep soil moisture or resprout success, and greater exposure to nighttime radiation freezes after canopy removal by fire. *Ceanothus megacarpus, C. spinosus,* and *Malosma laurina* dominate the non-freezing landscape of coastal exposures, whereas *C. crassifolius* and *Rhus ovata* dominate inland cold air drainages. Because *C. spinosus* and *M. laurina* form lignotubers they can persist immediately upslope of cold valleys through vegetative resprouting after periodic freeze-induced death of shoots. Because *C. megacarpus* and *C. crassifolius* are not capable of vegetative resprouting (non-sprouters after shoot death by freezing), they are either eliminated from cold inland sites (*C. megacarpus*) or are adapted to freezing in combination with drought (*C. crassifolius*). In some cases, stems are more susceptible to freezing induced dysfunction than leaves (*R. ovata*) whereas in other species, both stems and leaves are extremely resistant to freezing-induced dysfunction, even when partially dehydrated

(*C. crassifolius*). In the case of *M. laurina*, both stems and leaves are susceptible to freezing with total shoot dieback at -6 °C. However, stunted individuals of *M. laurina* may persist at -9 °C sites in the Santa Monica Mountains through repeated resprout success. We conclude that a suite of factors, such as resprout success, the susceptibility of leaves and stem xylem to freezing injury, and the interactions of drought and freezing, contribute to the final distribution patterns of chaparral species in the Santa Monica Mountains.

KEYWORDS: Freezing, xylem, cavitation, LT_{50}, Chaparral, *Malosma, Rhus, Ceanothus*

INTRODUCTION

Chaparral is a dominant vegetation type in the Santa Monica Mountains of southern California. Differential distribution of chaparral species along elevational gradients and in response to slope, aspect, and hill-valley effects in the Santa Monica Mountains and associated Transverse Mountain Ranges has primarily been attributed to differences in moisture availability and exposure to solar radiation (Harrison et al. 1971, Nicholson 1993, Davis et al. 1999a, Meentemeyer et al. 2001, Moody and Meentemeyer 2001). Here we focus on the neglected topic of freezing air temperatures as a possible determinant of chaparral species distribution in the Santa Monica Mountains (cf. Ewers et al. 2003, Davis et al. 2005).

CHAPARRAL DISTRIBUTION AND FREEZING TEMPERATURES

Differences in daily minimum air temperatures from coastal to inland regions of the Santa Monica Mountains often exceed 10 °C (Figure 1A). Shrub species that dominate coastal exposures (*Malosma laurina, Ceanothus megacarpus, C. spinosus*) are rare to infrequent just a few kilometers inland, especially in low-lying valleys (Figure 1B). Surprisingly, species that typically occur at higher elevations of the Transverse Mountain Ranges (e.g. *C. crassifolius, C. oliganthus, Rhus ovata*) are found in the Santa Monica Mountains to occupy lower elevations (cf. Nicholson 1993, Meentemeyer et al. 2001, Moody and Meentemeyer 2001). These same valleys experience cold air drainages and nighttime temperatures that may dip below -11 °C (Figure 1B).

The observed temperature extremes between coastal and inland sites may impact distribution patterns of chaparral species. Figure 2 displays two photographs taken of the same interior, Northeast-facing slope of the Santa Monica Mountains on two different dates, 4 March 2003 and 29 April 2003. These two photographs correspond to the vegetation gradient diagramed in Figure 1B. Peak floral display on the upper slope in March is *C. megacarpus* (Figure 2A). Peak flowering seen on the lower slope in April is *C. crassifolius* (Figure 2B). On close inspection of Figure 2B, lavender colored flowers, restricted to upper slopes, indicate the location of *C. spinosus* (Figure 2B). Why is *C. megacarpus* absent from lower elevations, where it is replaced by *C. crassifolius*, a species that typically occupies high elevations in the Transverse Mountain Range (Nicholson 1993, Meentemeyer et al. 2001)? Why is *C. spinosus*, which typically occupies moist ravines (Schlesinger et al. 1982) and low elevations, absent from the valley floor where it is replaced by what is normally higher elevational *C. oliganthus* (Nicholson 1993, Meentemeyer et al. 2001)? Why is *M. laurina* excluded from the valley floor and apparently displaced by a morphologically similar member of the Anacardiaceae family, *Rhus ovata*? One possibility is that inverted freezing gradients, due to cold air drainage, regulate this pattern (Figure 1A, B).
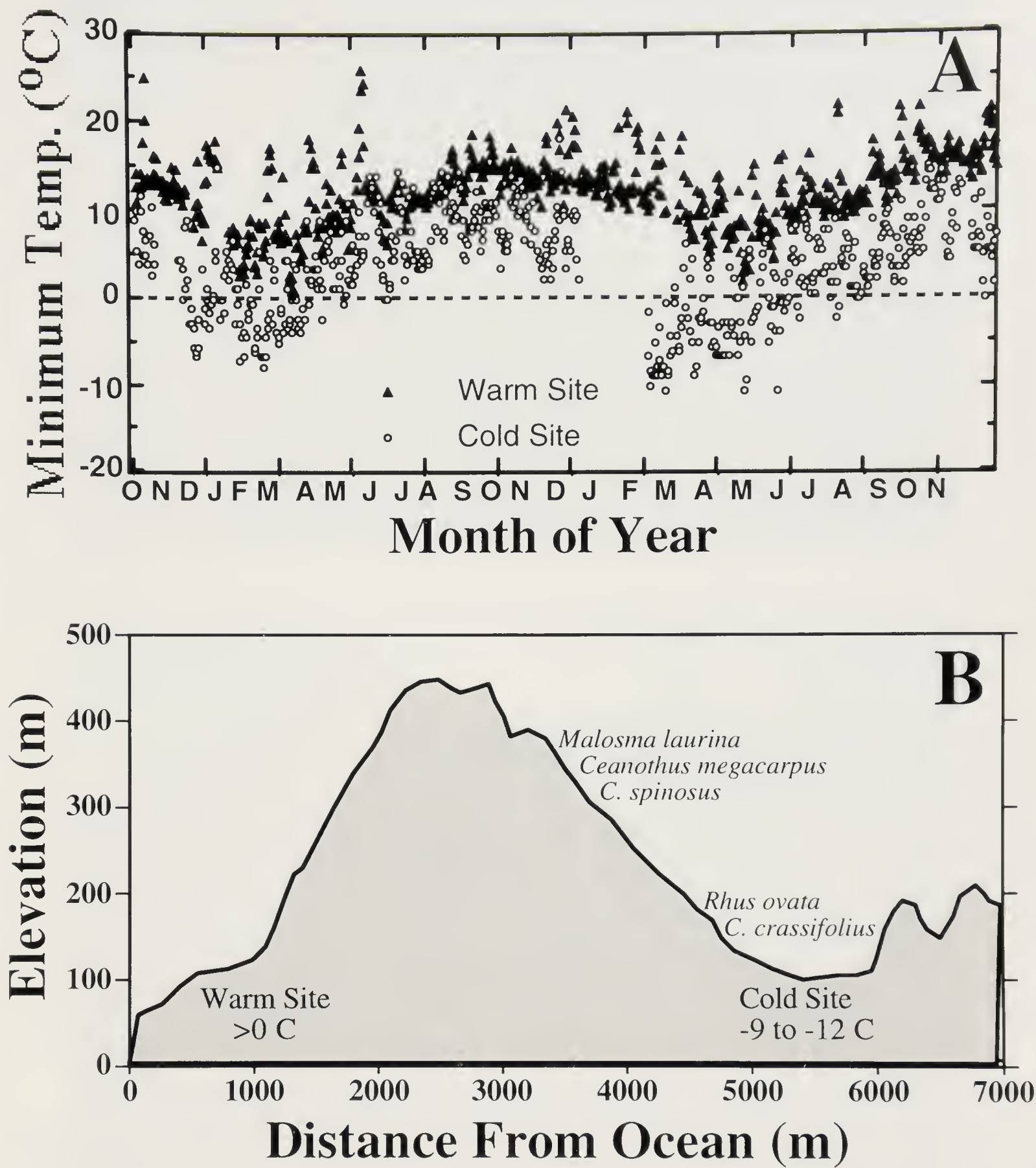
Figure 1. A) Minimum daily temperatures measured at a "Warm Site", coastal exposure, of the Santa Monica Mountains (modified from Boorse et al. 1998b). The site was located in a mixed chaparral stand on the Pepperdine University campus in Malibu at an elevation of 165 m. The "Cold Site" was located about 6 km inland, at the Malibu Forestry Unit of Los Angeles County Fire Department, just off Malibu Canyon Road, at an elevation of 195 m. **B)** Diagram illustrating approximate distance, topography, elevation, and species distribution of plants shown in Figure 2 and relative position of the warm and cold study sites (modified from Davis et al. 2005).
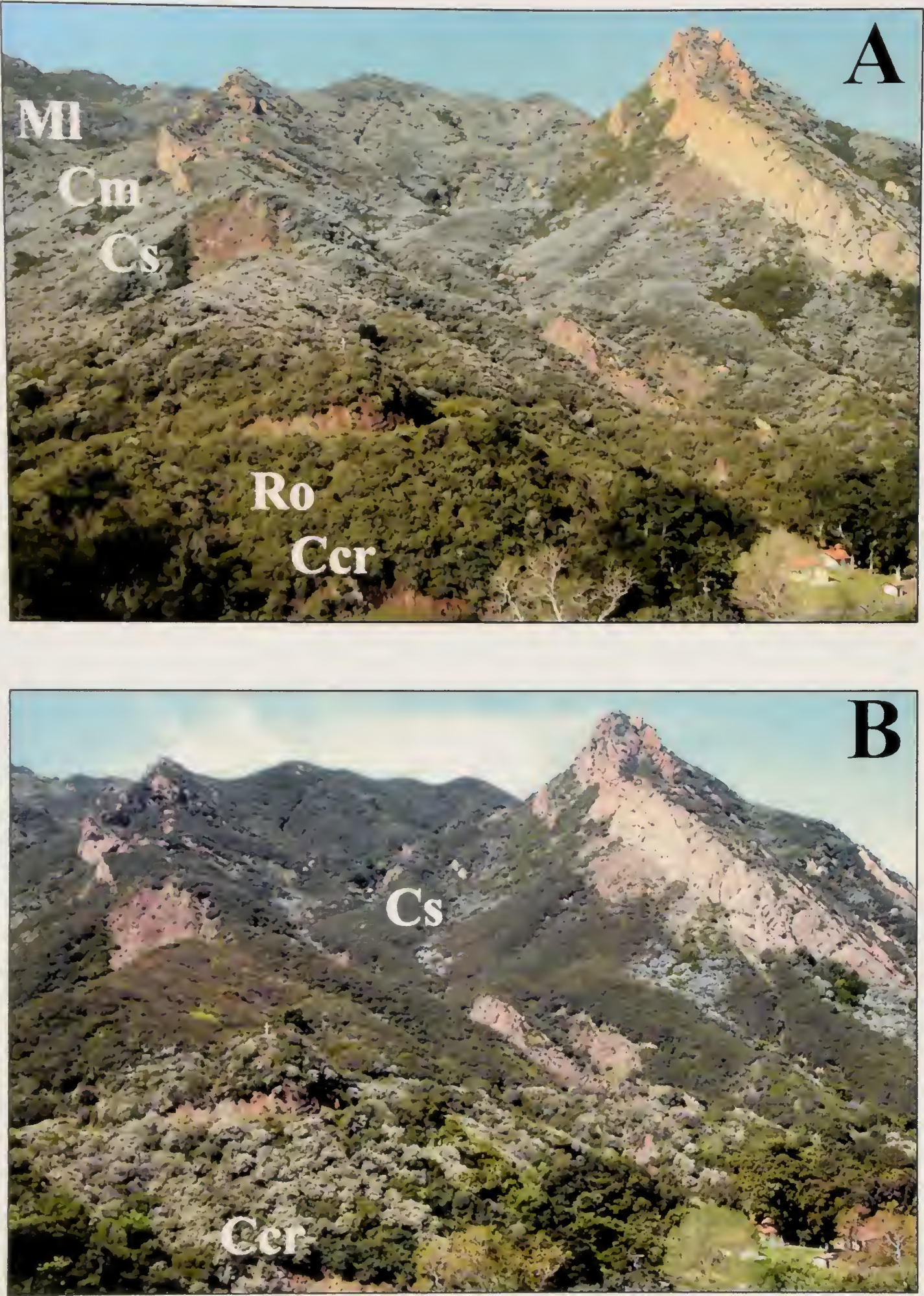
Figure 2. A) Photograph taken 4 March 2003 of the Northeast-facing slope of the Santa Monica Mountains, about 5 km inland from the coastline. Photograph taken from Tapia Park with the Salvation Army Camp in the foreground. *Ceanothus megacarpus* is in peak bloom on the upper slope (white inflorescence). *C. crassifolius* and *C. spinosus* are not yet in bloom. Letters stand for Ml = *Malosma laurina*, Cm = *C. megacarpus*, Cs = *C. spinosus*, Ccr = *C. crassifolius*, and Ro = *Rhus ovata*. **B)** Same photograph as in "A" above, but taken 29 April 2003. Note that *C. crassifolius* is in peak bloom on lower slopes (white inflorescence) and *C. spinosus* is in peak bloom, in moist ravines on upper slopes (lavender inflorescence).

At a finer scale than shown in Figure 1, very near the site pictured in Figure 2, we installed thermocouples, spring loaded to place them in physical contact with leaves in the upper and lower canopy of *M. laurina* and *R. ovata* and recorded daily changes in temperature between hillcrest and valley floor (Figure 3B; Langan et al. 1997). Lowest temperatures were observed just prior to dawn on calm, clear nights, consistent with the occurrence of radiation freeze and cold air drainage, and were 4 to 5 ºC lower in the valley than on the hillcrest (Figure 3A, B). Adult *M. laurina* experienced freezing dieback, especially in upper canopy leaves, whereas *R. ovata* did not (Figure 3A, C). Adult *M. laurina* resprouted vigorously from root crowns and thus were not eliminated from the hillcrest but persisted, albeit stunted in growth (Figure 3C). This was not the case for seedlings of *M. laurina* that experienced 100% mortality after a -7 ºC-freezing event on 28 December 1997 (Figure 4). Presumably, *M. laurina* on the hillcrests produced seeds that were carried downhill into the valley by surface erosion and were promoted to germinate by the effects of wildfire in the fall of 1996 (Pratt et al. 2005). However, in the subsequent fall of 1997, newly germinated seedlings of *M. laurina* experienced increasing freezing injury to leaves as temperatures declined (estimated by dark adapted chlorophyll fluorescence, Fv/Fm; Figure 4B). Eventually, after experiencing leaf temperatures of -7.2 ºC on Julian Day 362 (28 December), there was 100% mortality of seedlings on the valley floor (Figure 4B, C, D). Presumably, post-fire seedlings did not have sufficient time to develop root crowns to facilitate resprouting after freezing injury, which is typical for adults. Thus none of the seedlings that initially germinated on the valley floor survived (Pratt et al. 2005). Adjacent seedlings of *R. ovata* were uninjured by the -7 ºC freezing event and unlike *M. laurina* recruited new individuals into the valley population after the wildfire of 1996 (Figure 4B; Pratt et al. 2005).

These results for the Santa Monica Mountains are consistent with previous observations on a broad geographical scale for southern California. Misquez (1990) found *M. laurina* to experience greater freezing damage when located in valley bottoms than upper slopes. She reported 95% canopy damage at valley bottoms, 72% on lower slopes, and 18% on upper slopes. She found *M. laurina* to be entirely absent from low altitude basins near Campo and Elsinor California and in the Perris Plain south of Riverside she reported that "*M. laurina* is found only on summits and flanking slopes of hills above the level of ground inversions that normally overlie the basin" (Misquez 1990, page 29). This hill versus valley displacement is also consistent with the restricted distribution of *M. laurina* to warm microsites and coastal exposures from Baja California to its northernmost extension in San Luis Obispo County, California (cf. Mooney 1977, Keil et al. 1985, Misquez 1990).

This hill versus valley displacement is somewhat paradoxical because newly germinated seedlings of *M. laurina* typically demonstrate low survivorship in response to water stress and would normally benefit from increased soil moisture in valley bottoms. In two separate studies at warm coastal sites shown in Figure 1B, we found seedling survivorship to range between 0.6 and 1.1 % during the first summer drought after wildfire (Frazer and Davis 1988, Thomas and Davis 1989). After the summer drought of 1997 at our inland cold site (Figure 1B), *M. laurina* seedlings shown in Figure 4A had a survivorship of 7.5% (unpublished data), significantly higher than typical, presumable due to greater moisture availability in the valley floor. However, by the end of December 1997, these same *M. laurina* seedlings had 0% survivorship on the valley floor because of the additive effects of freezing-induced mortality (Figure 4B). It is also paradoxical that resprout success after freezing is probably more significant for persistence than resprout success after wildfire. This is because freezing-induced dieback occurs every 3 or 4 years whereas fire events occur on average about once every 21 years (Radkte et al.1982). A third underappreciated paradox is that decreasing air temperature with elevation, based on a typical lapse rate of -5 °C per 1000 m (Nobel 1999) is much lower in magnitude and in the reverse
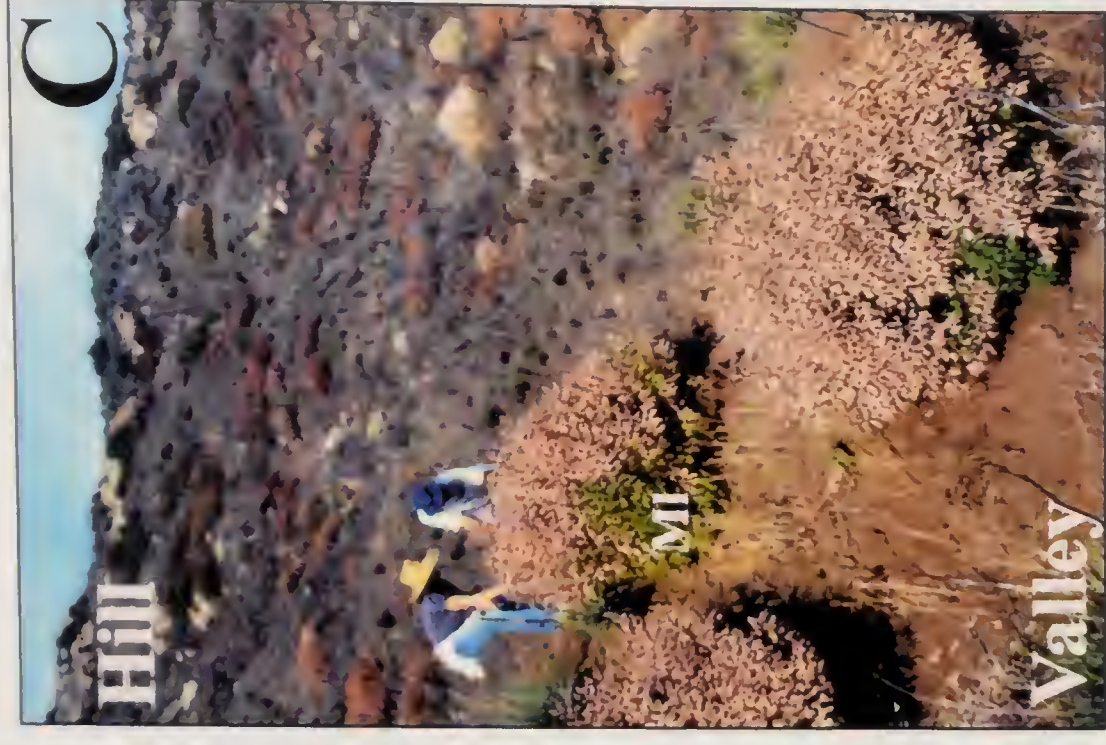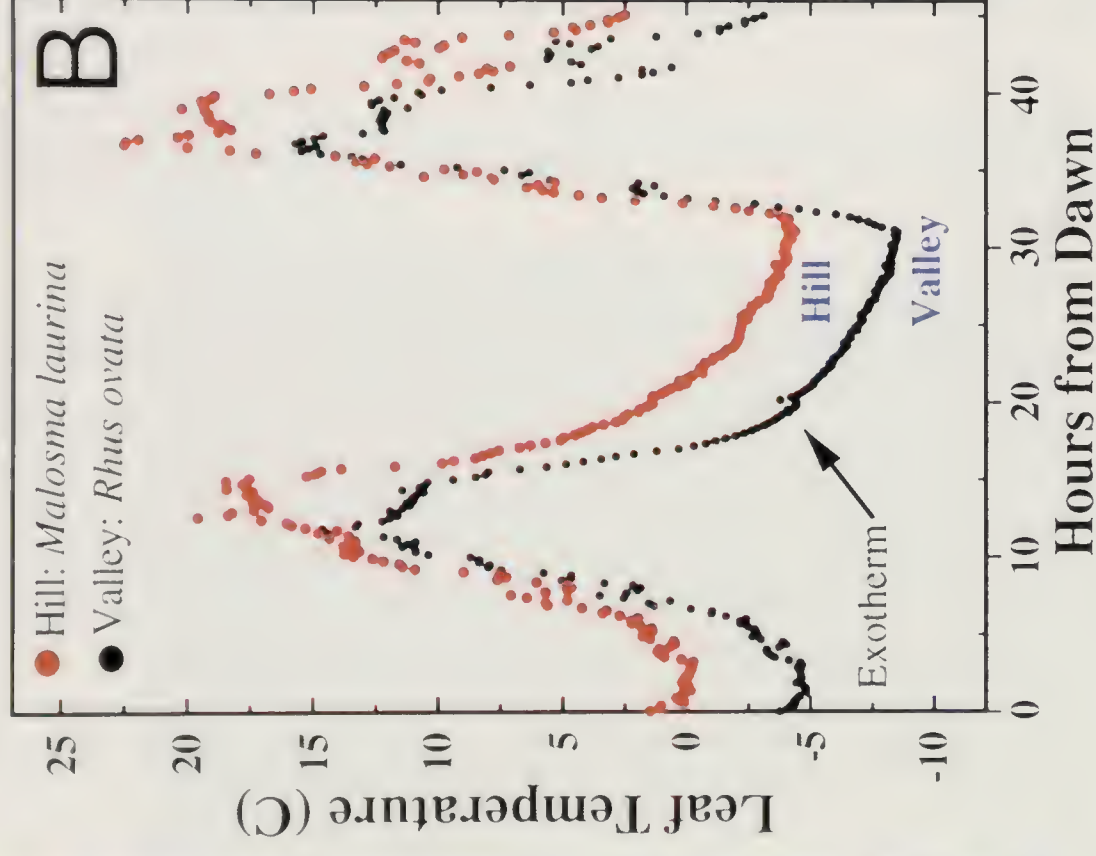
Figure 3. A) Photograph taken of "hill and valley effects" at the Malibu Forestry Unit of Los Angeles County Fire Department, just off Malibu Canyon Road, in January of 1993, about one month after a nighttime freezing event of 19 and 20 December 1992 (shown in Figure 3 B). Letters stand for Ml = *Malosma laurina*, Ccr = *C. crassifolius*, and Ro = *Rhus ovata*. Red plants near the hillcrest represent shoot dieback among *M. laurina* after the nighttime freezing event (modified from Langan et al. 1997) **B)** Thermocouples placed on leaves of *M. laurina* (hill: in red symbols) and *R. ovata* (valley: in black symbols) indicated 4 to 5 ℃ lower minimum temperature in the valley. Note the exotherm that indicates freezing of plant tissues occurred in the valley at about −5 ℃ but did not occur on the hillcrest. Data shown for 19 and 20 December 1992, modified from Langan et al. 1997. **C)** Hill and valley gradient at Tapia Park, adjacent the Malibu Forestry Unit shown in Figure 3A. Note stunted form of *M. laurina*, leaf dieback due to freezing, and evidence of resprout success near the base of dead shoots (Label "Ml" = *Malosma laurina*).
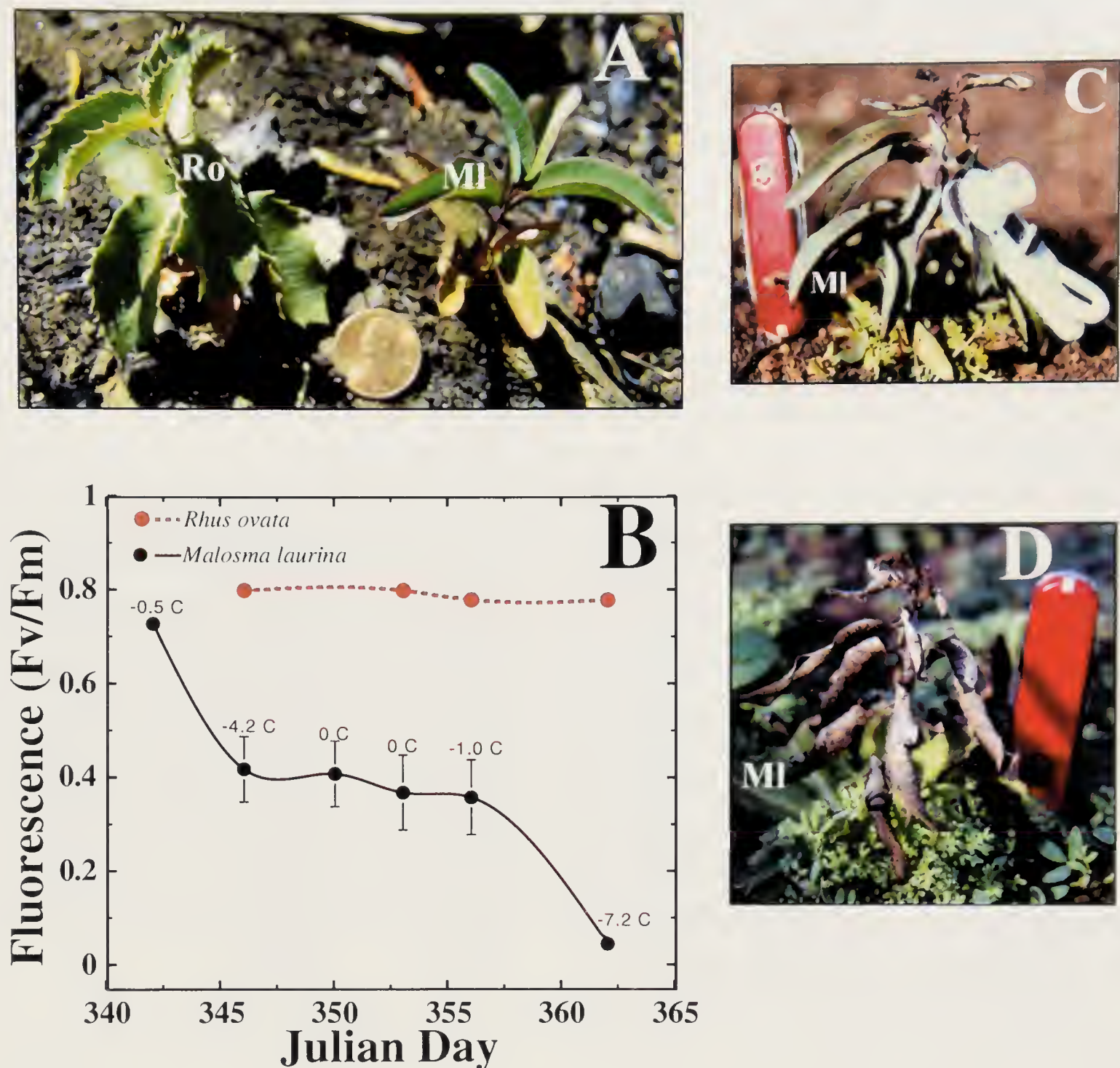
Figure 4. A) Seedlings of *Rhus ovata* (labeled Ro) and *Malosma laurina* (labeled Ml) that germinated adjacent each other, in the valley floor near Tapia Park, after the wildfire of 1996. *Malosma laurina* seedlings persisted in the valley until the first freezing event occurred in December 1997 (cf. Figure 4B). B) Dark adapted chlorophyll fluorescence on leaves of *Rhus ovata* and *Malosma laurina* seedlings growing in the valley floor at the Malibu Forestry Unity in late fall of 1997. Temperatures by black symbols indicate minimum leaf temperatures measured the night before each Fv/Fm determination. None of 12 *M. laurina* seedlings survived the freezing exposure of -7.2 °C whereas all 10 *R. ovata* seedlings survived (modified from Pratt et al. 2005). C) Photograph of a *M. laurina* seedling (labeled Ml) taken the day after a -4.2 °C freezing event showing partial injury assessed by a dark-adapted cuvette for Fv/Fm determination. D) Same seedling one month after a freezing event of -7.2 °C. Like all 12 seedlings measured, the seedling shown did not resprout or survive. There was 100% mortality of seedlings in the valley floor.

direction to hill-valley temperature gradients in the Santa Monica Mountains (+5 °C per 100 m, Figure 3B). Furthermore, coastal to inland minimum temperatures, just 6 km apart, at the same elevation, may differ by as much as 12 °C in the Santa Monica Mountains (Figure 1B).

PHYSIOLOGICAL TOLERANCE TO FREEZING TEMPERATURES

To understand the physiological mechanisms driving chaparral distribution patterns in response to freezing, we employed several types of controlled laboratory experiments: 1) we assessed the lethal temperature that caused 50% mortality (LT_{50}) of leaf cells by four different methods (Boorse et al. 1998a, 1998b); 2) we used a freezing chamber to simulate freeze thaw cycles experienced by shrubs at our field sites and measured impacts on both leaves (LT_{50}) and stems (freezing-induced xylem cavitation) (Langan et al. 1997, Ewers et al. 2003, Pratt et al. 2005); and 3) we employed a freezing-centrifuge technique to separate the effects of water stress and freezing on xylem embolism (Davis et al. 1999b, Davis et al. 2005).

Consistent with field observations and chaparral distribution patterns, results of our LT_{50} experiments showed that leaves of *M. laurina* were more susceptible to freezing injury (LT_{50} -6 °C) than *C. megacarpus* (-10 °C) and *C. spinosus* (-9 °C) and dramatically more susceptible than *Rhus ovata* (-16 °C) and *C. crassifolius* (-18 °C) (Figure 5A, Boorse et al. 1998a, Boorse et al. 1998b, Ewers et al. 2003, Davis et al. 2005). Leaf level results were consistent with observed distribution patterns from coastal to inland sites (Figure 1A, B), inverted freezing gradients into cold air drainages (Figure 1B; Figure 2A, B; Figure 3A, C), and differential mortality of seedlings (Figure 4B). When leaf-freezing injury was compared between warm coastal sites and cold inland sites (Figure 6A), leaves at cold sites had lower LT_{50} suggesting ecotypic variation between coastal and inland populations (Boorse et al. 1998b). When leaf-freezing injury was compared between summer and winter, winter leaves were most resistant, indicating seasonal hardening (Figure 6B). When leaf-freezing injury was compared between seedlings and adults (Figure 6C), adult leaves were found to be more resistant (lower LT_{50}), suggesting that freezing effects on seedlings during establishment may be a primary determinant of final chaparral distribution patterns in the Santa Monica Mountains (cf. Figure 3A, 4B).

Freezing-chamber experiments on whole branches of *M. laurina* showed that stem xylem was as susceptible as leaves to freezing injury (Figure 5A, B). Freezing stems below -6 °C resulted in nearly 100% embolism, indicating total blockage of water transport to leaves. Thus both freezing injury to leaves and freezing-induced embolism of stem xylem contributed to the shoot dieback of *M. laurina* observed at field sites after freezing events (cf. Figure 3C). This was not the case for *C. megacarpus, C. spinosus,* and *C. crassifolius*. Under hydrated conditions, leaves were more susceptible to freezing injury (LT_{50} = -9 °C for *C. megacarpus* and *C. spinosus* and -18 °C for *C. crassifolius*) than stems (resistant to -20 °C; cf. Langan et al. 1997, Ewers et al. 2003). However, if stems were dehydrated to -5 MPa and then frozen, which is not uncommon in late fall when late seasonal drought coincides with the onset of winter freezing, *C. megacarpus* and *C. spinosus* became highly susceptible to freezing-induced embolism (Figure 5B). This was not the case for *C. crassifolius,* which remained the most resistant to freeze-induced cavitation of stem xylem in addition to having the lowest LT_{50} of leaves (Figure 5B; Davis et al. 2005). This pattern is consistent with the dominance of *C. crassifolius* in cold air drainages in the Santa Monica Mountains and its occurrence at higher elevations in the Santa Ynez and San Gabriel Mountains (Nicholson 1993, Meentemeyer et al. 2001). The only apparent inconsistency in our data comparing freezing tolerance to chaparral species distribution is for *Rhus ovata*. Although leaves of *R. ovata* tolerate temperatures well below -12 °C (LT_{50} = -16 °C; Figure 5A), stem xylem undergoes > 95% embolism after a single freezing event of -6 °C (Figure 5B; Pratt et al. 2005). How can this species flourish in cold air drainages shown in Figures 1 and 2 and displace its
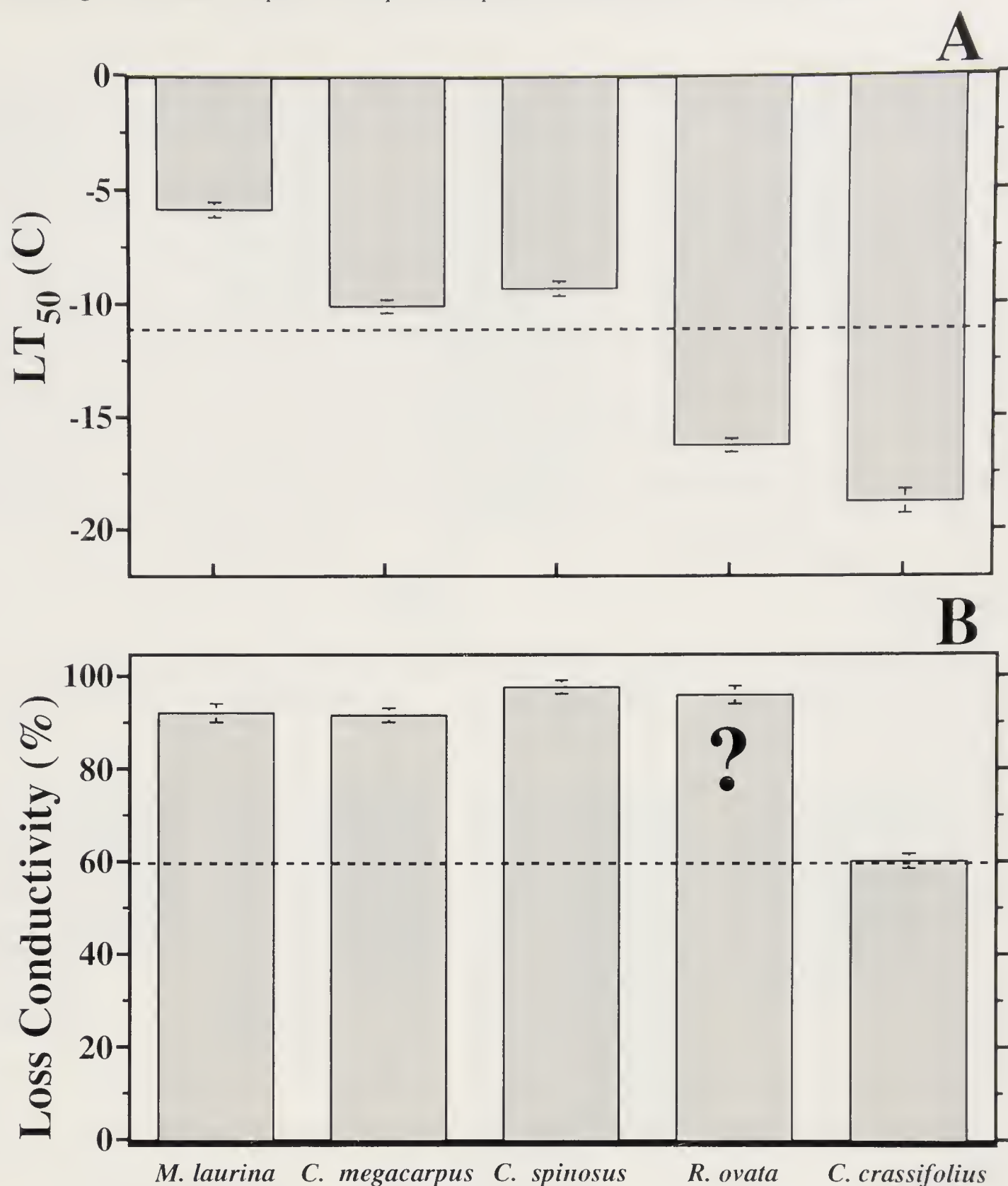
Figure 5. A) Leaf temperature at 50% cell death of leaf palisade parenchyma using fluorescein diacetate vital stain in conjunction with an epifluorescence microscope for *Malosma laurina, Ceanothus megacarpus, C. spinosus, Rhus ovata*, and *C. crassifolius*. Error bars on symbols are ± 1 SE, N = 6. As a reference, the dashed line represents -11 °C air temperature shown in Figure 1A (adapted from Davis et al. 2005). **B)** Effect of freeze-thaw treatments on excised, > 2 m long branches, placed in a freezing chamber that simulated the freeze thaw cycle observed in the field at our cold study site (Figure 3B). To represent typical field conditions, *M. laurina* and *R. ovata* were hydrated (-0.5 MPa water potential) whereas *C. megacarpus, C. spinosus*, and *C. crassifolius* were partially dehydrated (-5.0 MPa water potential). As a reference, the dashed line shows a modest embolism level of 60% for *C. crassifolius* in comparison to all other species. The question mark indicates an apparent inconsistency in correlating physiological data to chaparral species distribution in the Santa Monica Mountains. That is, *R. ovata* occurs at cold sites but experiences high freezing-induced embolism (adapted from Davis et al. 2005).
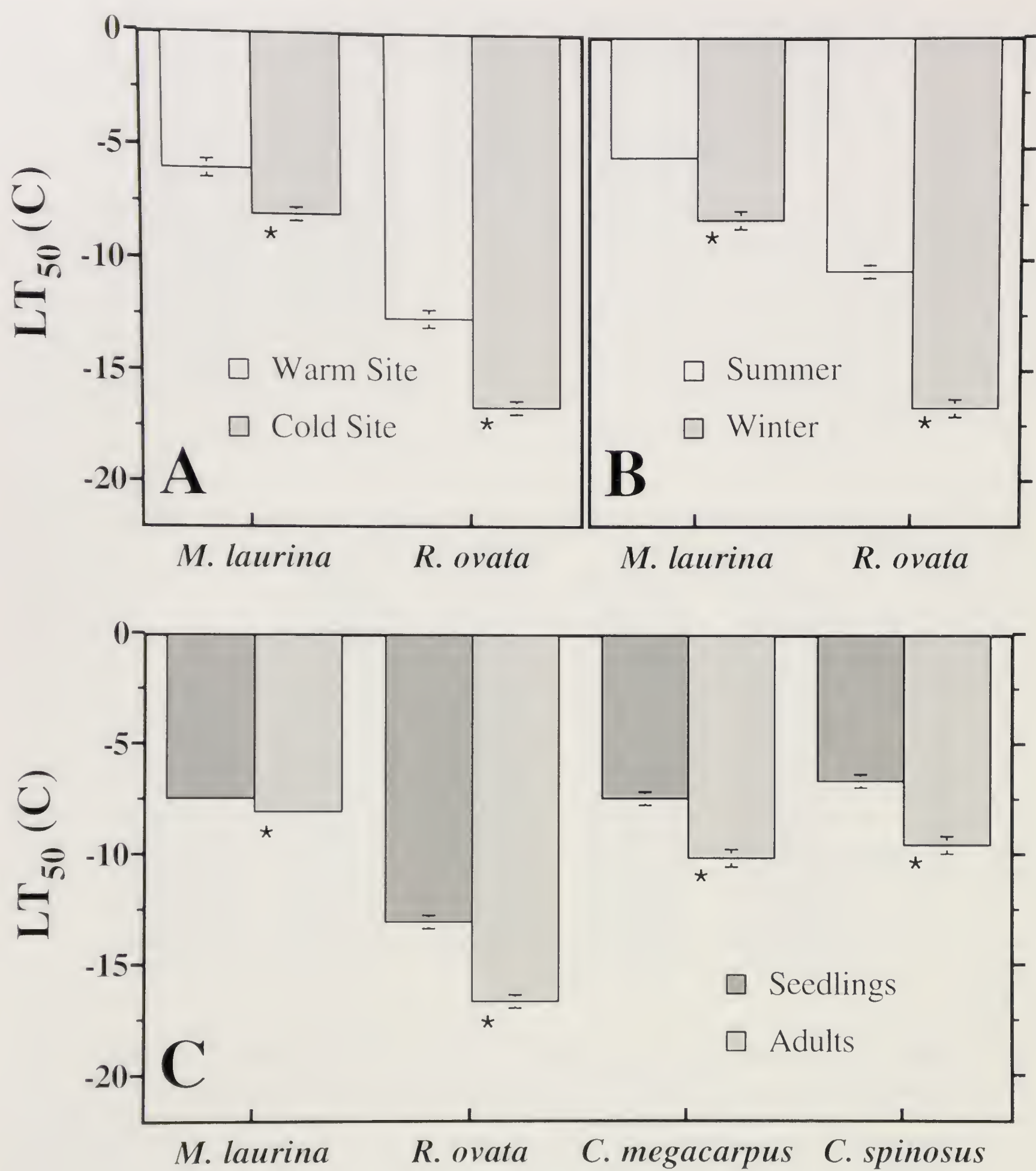
Figure 6. A) Changes in LT_{50} (leaf temperature at 50% cell death by fluorescein diacetate vital stain) between *Malosma laurina* and *Rhus ovata* adults located at our warm and cold sites shown in Figure 1B. Bars represent ± 1 SE, N = 5. Asterisks on adjacent bars represent significant difference by unpaired Student's t test at P < 0.05 (adapted from Boorse et al. 1998b). **B)** Differences in LT_{50} between *M. laurina* and *R. ovata* at our cold site during summer and winter months (adapted from Boorse et al. 1998b). **C)** Differences in LT_{50} between seedlings and adults of *M. laurina*, *R. ovata*, *Ceanothus megacarpus*, and *C. spinosus* in winter months (adapted from Boorse et al. 1998b).

closest relative, *M. laurina*? Is it possible that *R. ovata* experiences high embolism of stem xylem yet retains evergreen leaves because of unusually high water conservation ability? We tested this possibility by comparing water loss rates and chlorophyll fluorescence (Fv/Fm) of excised leaves of *R. ovata* to *M. laurina* in controlled environmental chambers. Consistent with our water conservation hypothesis, *R. ovata* leaves conserved water and retained fluorescence viability nearly 5-fold longer than did *M. laurina* leaves (retained Fv/Fm viability for ~5 day versus ~1 day: Figure 7A, B). Thus it appears that *R. ovata* flourishes in cold inland valleys of the Santa Monica Mountains by having leaves that are not only resistant to freezing injury (LT$_{50}$ = -16 °C; Figure 5A) but that are also exceptional in water conservation compared to leaves of *M. laurina* and many other species we have tested (Figure 7, data shown only for *M. laurina* and *R. ovata*). Evidently, *R. ovata* undergoes high xylem embolism at cold inland sites each winter but maintains sufficient leaf hydration to insure survival until the vascular cambium lays down new xylem in late winter and restores hydraulic supply, facilitating spring growth (Pratt et al. 2005).

CONCLUSIONS

While it is true that chaparral species distributions in the Santa Monica Mountains and associated Transverse Mountain Ranges are to some extent correlated with moisture availability, solar radiation, and fire patterns, it is likely that freezing air temperatures also play a causative role in distribution patterns. Obviously there are suites of factors during the life cycle of chaparral species that determine final habitat preference and niche segregation. The regeneration niche during seedling establishment and post-disturbance reprouting may be particularly important (Davis 1991). We have established at least one incident where 100 % freezing mortality of newly germinated seedlings precluded *M. laurina* occurrence in a cold inland valley of the Santa Monica Mountains. Once seedlings establish, on warmer hillcrests, *M. laurina* persists through vigorous resprouting, about every 21 years or so after wildfires but every three or four years after freezing events. Thus freezing events may be more crucial to persistence than wildfires at such sites. Seedlings may establish at hillcrests when post-fire germination is followed by three or more years of minimum seasonal temperatures > -6 C. We suspect that three years of growth is prerequisite for adequate root crown development and resprout success after freezing. It is unlikely that post-freezing resprout success would be possible in cold valleys where minimum temperatures are 4 to 5° C colder than hillcrests.

Based on recent predictions from climate models, it should be noted that the distribution patterns in the Santa Monica Mountains presented here might change. Global warming is predicted to have a greater impact on nighttime sky temperatures, than on maximum air temperatures or average air temperatures. Thus radiation freezes on calm, clear nights are predicted to decrease in frequency and intensity, especially in western regions of the United States (Frich et al. 2002; Meehl et al. 2004). Furthermore, global warming is predicted to promote more frequent and larger wildfires, also predominantly in western regions of the United States (Westerling et al. 2006; Running 2006). Taken together, it is probable that cold sensitive species that are also vigorous resprouters after wildfire, such as *M. laurina* and *C. spinosus*, will expand their range in the Santa Monica Mountains, in response to ongoing changes in climate for California.
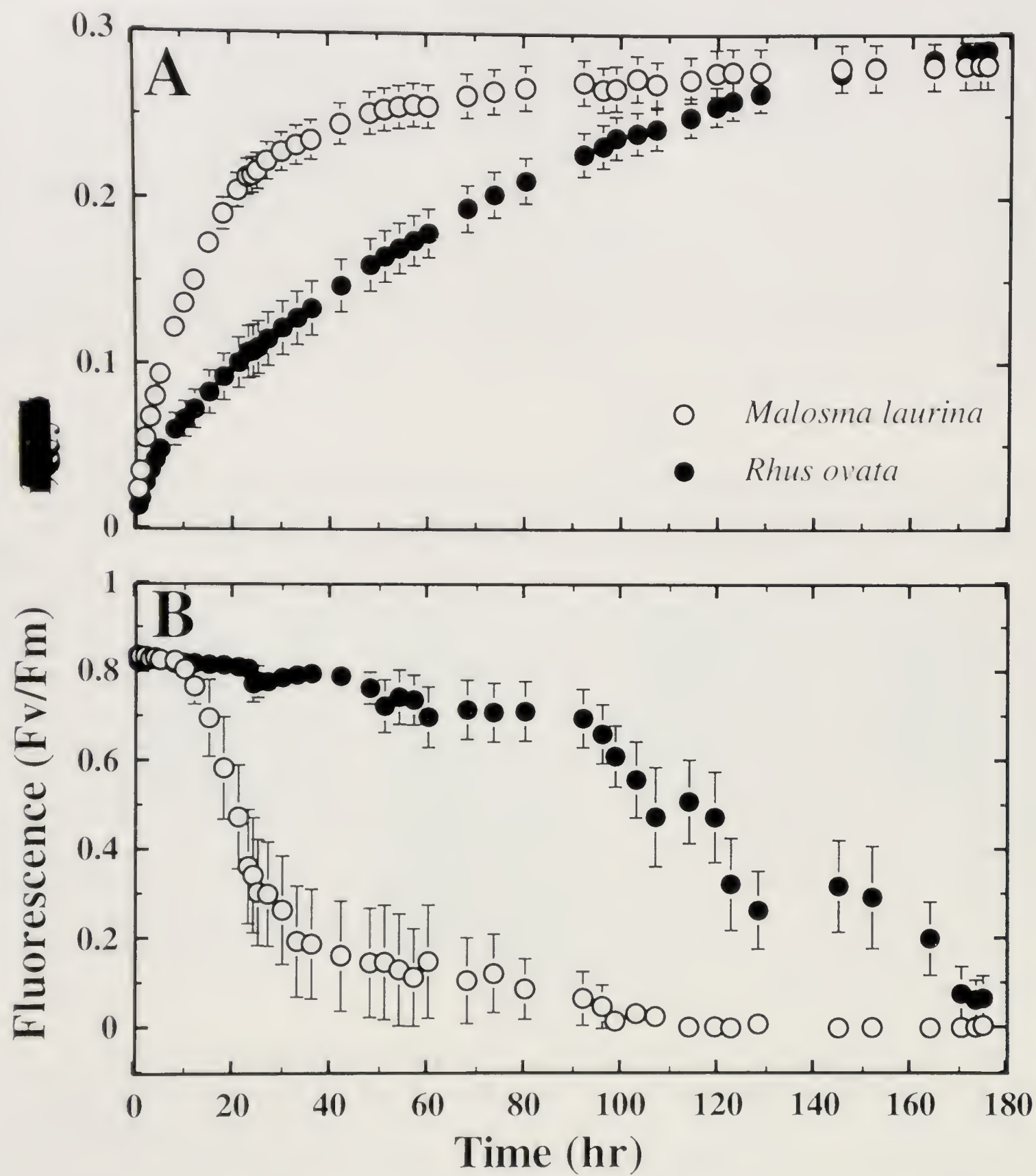
Figure 7. A) Water loss per unit leaf area and **B)** dark-adapted chlorophyll fluorescence (Fv/Fm) for *M. laurina* and *R. ovata*. Data were collected on excised leaves in which petioles were sealed with epoxy and allowed to dehydrate in growth chambers at 21.5 °C and a VPD (vapor pressure difference between the leaf and air) of 0.95 kPa for 7 days (adapted from Davis et al. 2005).

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VEGETATION RESPONSE TO WILDFIRE AND FIRE HISTORY IN THE SANTA MONICA MOUNTAINS, CALIFORNIA

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ABSTRACT: The most significant local factors controlling vegetation distribution and plant diversity in the Santa Monica Mountains are wildfire and the extended summer dry period associated with a Mediterranean-type climate. Fire is an inevitable recurring event because of the combination of vegetation type, climate, topography and land use. Both the number of fires and the total amount of area burned is increasing in the Santa Monica Mountains and elsewhere in the mountain foothills surrounding urban southern California. Altered fire regimes are resulting in profound changes in vegetation assemblages and structure and, in the most extreme cases, vegetation-fire feedback cycles resulting in the extirpation of native shrub species and vegetation type conversion. We review the fire history of the Santa Monica Mountains and describe how altered fire regimes, plant life histories, and plant physiological traits interact to affect landscape-level vegetation patterns.

KEYWORDS: fire, chaparral, drought stress, type conversion, life history, sprouter, seeder, southern California, recruitment, survival

INTRODUCTION

The Santa Monica Mountains have one of the most extreme fire climates in the world and periodically burn in large, dramatic wildfires (NPS 2005). Approximately 13% of this fire-prone area is developed, with communities that are among the wealthiest in Los Angeles County and the state of California. Fires in this region are often extremely damaging and costly because of both wildfire suppression costs and property losses, and are usually considered to be major social disasters. In contrast, biologists have considered fire in the Santa Monica Mountains to be a normal event that maintains the vigor and diversity of its shrubland plant communities. Chaparral is the classic example of an auto-successional cycle where wildfire burns all of the aboveground vegetation and at the same time stimulates the regeneration of the same species that grew there previously from both the soil seed bank and resprouting shoots (Hanes 1971). The observed resilience of chaparral to fire has led to the sometimes uncritical acceptance of the idea that any fire, any time, and any where is good for chaparral. Plants are not adapted to fire per se, but to a specific fire regime defined by the range of variability in fire type, season, size, frequency, and intensity. When the parameters of the fire regime exceed their normal range species can be extirpated, causing shifts in community composition and structure to occur. We have used an 80-year fire history of the Santa Monica Mountains to define the parameters of the local fire regime and to examine how changes in fire patterns have affected landscape-level vegetation patterns.

Changes in vegetation patterns as the result of altered fire regime parameters can primarily be explained by plant life history type and associated plant physiological traits.

THE MODERN FIRE REGIME

Setting and Climate

The Santa Monica Mountains are 90,000 hectares of isolated Mediterranean habitat bounded on one side by the Pacific Ocean and surrounded on three sides by the urban sprawl of greater Los Angeles. These mountains are the most southwestern of the east-west trending Transverse Ranges of Southern California. They extend from the Oxnard plain eastward for approximately 45 miles to the Los Angeles River. The steep and rugged slopes on the south flank of the mountains are cut by long, V-shaped, deeply incised canyons that drain south to the ocean. On the north flank, short steep canyons descend to the San Fernando and Conejo Valleys at about 1,000 feet above sea level. The exception is Malibu Canyon, a deeply incised, antecedent drainage course, which bisects the range, draining the north slopes of the Santa Monica Mountains and the southern slopes of the Simi Hills.

The dominant vegetation types are chaparral (55%) and coastal sage scrub (20%) which are particularly good fire fuels because of their high density and continuity, small twig and stem size, and the large proportion of dead biomass. The average total live and dead fuel biomass is 17 Mg/ha in *Adenostoma* chaparral, 36 Mg/ha in *Ceanothus*-chaparral and 20.2 Mg/ha in coastal sage scrub (Ottmar et al. 2000). The average annual rainfall is 430 mm/year, and falls predominantly between November and March with an extended dry season from May to October. Seasonal föehn winds (Santa Anas), averaging 30-50 kph, occur mostly in the fall months at the end of the dry season and are often associated with high temperatures and low humidity. The Santa Ana winds, which blow predominantly from the north or northeast, are funneled through the north-south canyons of the mountains. By the middle of fall, live fuel moisture is critically low (~ 60%, Figure 1). This combination of vegetation and climate make the Santa Monica Mountains, and Southern California in general, one of the world's most severe fire climates (Schroeder and others 1964). Digitized records of fires in the Santa Monica Mountains from 1925 to the present are maintained by the National Park Service. We have used these records to quantify the modern wildfire regime of the Santa Monica Mountains.
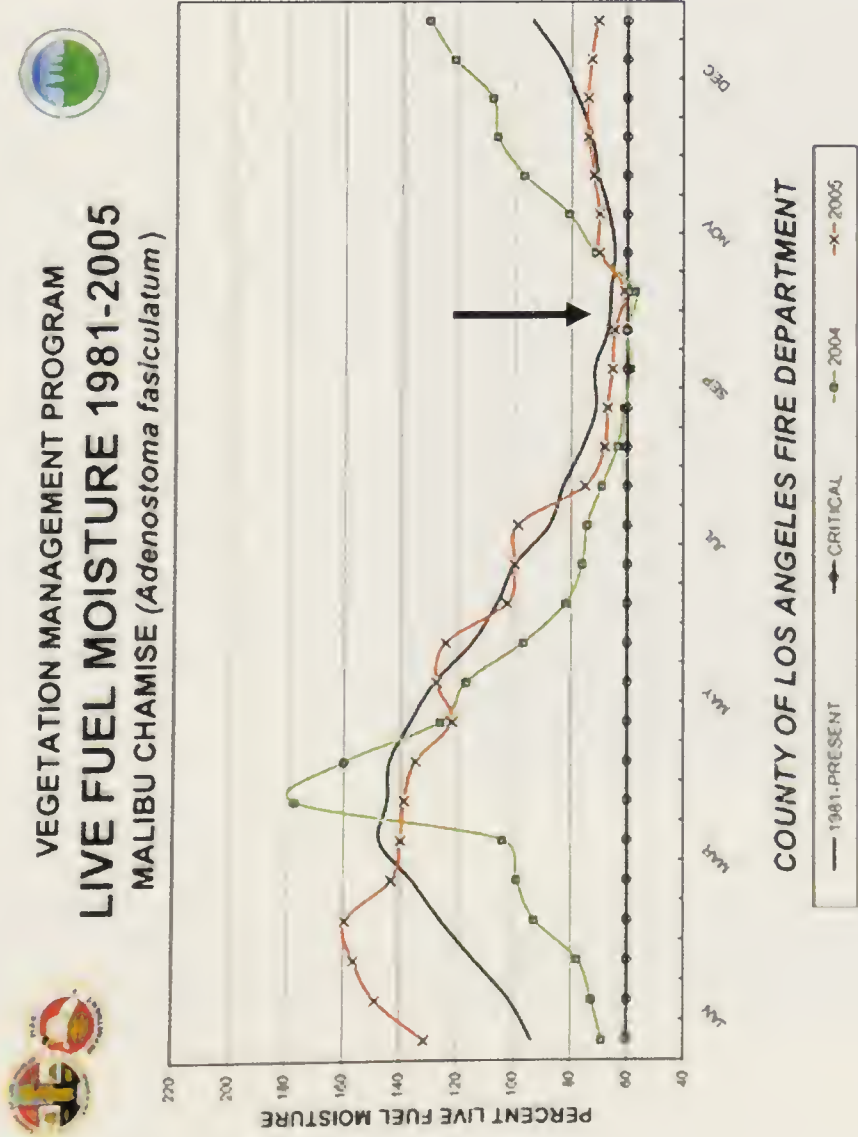
Fire Type

Fires in shrubland vegetation types such as chaparral and coastal sage scrub are high-intensity, stand-replacing crown fires. Type-converted shrublands with native shrubs growing in a non-native annual grassland matrix will experience a mixed fire type with cooler surface grass fires interspersed with high intensity canopy fires in native shrubs.
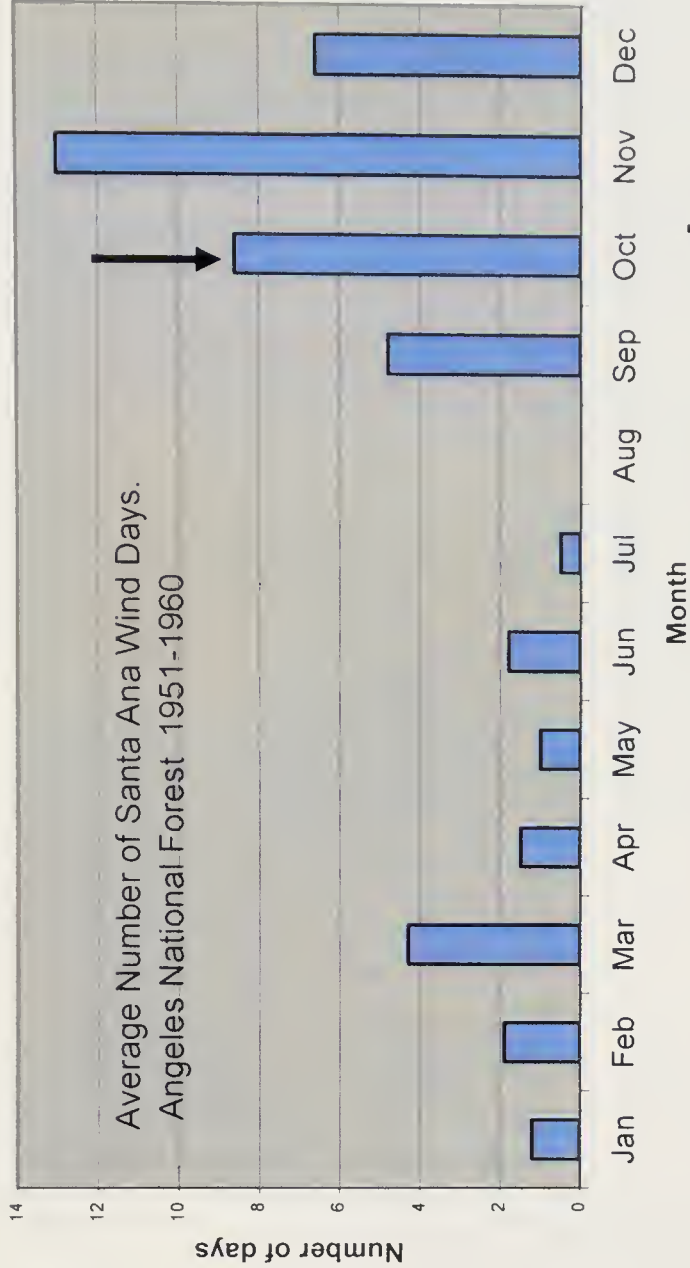
Fire Season

Föehn winds have been identified as the primary driver of the wildfire regime in southern and central California shrublands (Moritz 1997; Keeley and Fotheringham 2000). Although Santa Ana winds can occur in any month, they predominate from September to December (Figure 1B). The large fires in the Santa Monica Mountains coincide with this peak of Santa Ana activity when vegetation is dry and temperatures are high (Figure 1). Half of the area burned in the Santa Monica Mountains since 1925 burned in the month of October, while ninety percent burned between September and December (Figure 1C). A second small peak of Santa Ana wind activity

A.

VEGETATION MANAGEMENT PROGRAM
LIVE FUEL MOISTURE 1981-2005
MALIBU CHAMISE (Adenostoma fasiculatum)

COUNTY OF LOS ANGELES FIRE DEPARTMENT

1981-PRESENT   CRITICAL   2004   2005

B.

Average Number of Santa Ana Wind Days.
Angeles National Forest 1951-1960
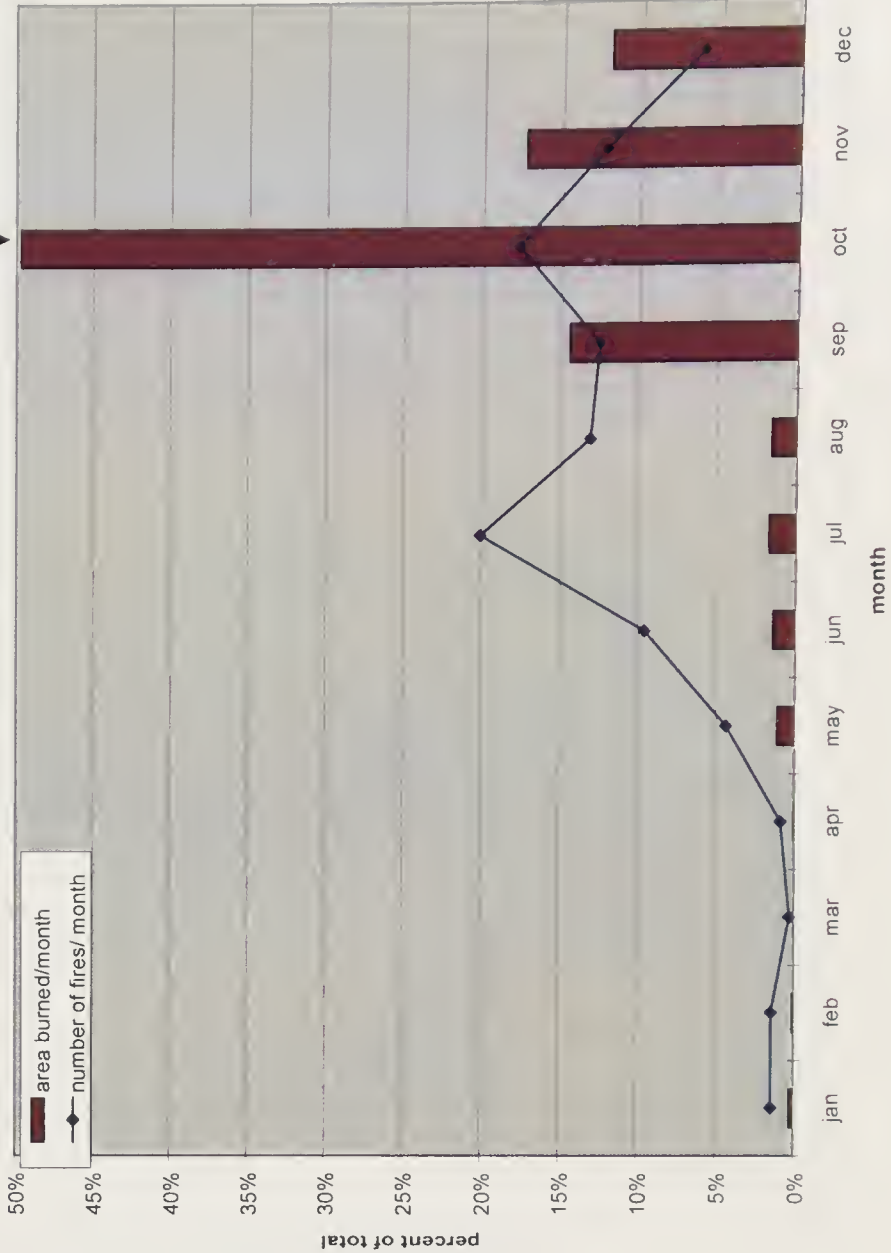
C.

area burned/month
number of fires/ month

Figure 1.

A. Seasonal live fuel moisture, Malibu
B. Average number of Santa Ana wind days/month
C. Percentage of total area burned /month and
percentage of total number of fires per month

occurs in March, but this is usually a time of cool temperatures and high moisture and does not create the severe fire conditions that lead to large, uncontrolled fall wildfires.

Ignition Sources

Lightning ignited wildfires are extremely rare in the Santa Monica Mountains. Only two clusters of lightning started fires, 14 years apart, have been recorded in a 25-year fire ignition record (1981-2006). Of these fires, the largest was 600 acres, while the others were only 0.1-0.2 acres in size.

Native Americans occupied the Santa Monica Mountains for approximately 10,000 years before present and are known to have used fire as a cultural tool, but both the frequency and geographic extent of their fire use are unknown (cf. references by Keeley 2002, *Journal of Biogeography* 29:303-320; references by Kat Anderson 1999, *Human Ecology*, 27:79-113). Currently, ninety-eight percent of all fire starts are of human origin, with arson and arcing power lines responsible for the vast majority of the total area burned (NPS 2005).

Fire Size

Large fires (greater than 10,000 acres) are responsible for nearly all of the area burned in the Santa Monica Mountains. The largest 1% of fires has caused 25% of the total burned area and the largest 10% have caused 86% of the total burned area (Figure 2). Large fires have occurred throughout the fire record period (Figure 3). This is consistent with data from the rest of southern California, where the number of large fires has not increased since modern fire suppression began and therefore cannot be a function of increased fuel accumulation (Keeley et al. 1999). Although the wildfire size distribution in the Santa Monica Mountains has remained largely stable over time, the trend in average fire size has declined very slightly from 1925 to the present (Schoenberg et al 2003).

Fire Frequency and Fire Return Interval

Fire frequency is the number of fires within a given area in a specific period of time, while the *fire return interval* is the period of time between fires within a given area in a specific period of time. Fire frequency has increased in the Santa Monica Mountains over the last 75 years (Figure 4). The total area burned per decade has also generally increased (Figure 5). Both of these trends are attributed to increased ignitions due to urbanization and increased population size (Keeley and Fotheringham 2001).

The average between-fire interval for all natural areas in the Santa Monica Mountains from 1925 to 2001 was 32 years. This statistic expresses the average time between fires for any set of randomly determined locations in the area. The fire return interval within the Santa Monica Mountains is widely variable because there are both high fire frequency areas that have burned numerous times in the 80 years of record keeping and areas that have never burned in that period. This creates a complex mosaic of fire history across the landscape (Figure 6).

Fire Spread Patterns and Fire Frequency

Fire spread patterns are strongly influenced by topography and the direction of the prevailing winds during Santa Ana conditions. There is often an east-west spread as fires travel from north to south approaching the coast and are released from the confines of steep north-south mountain
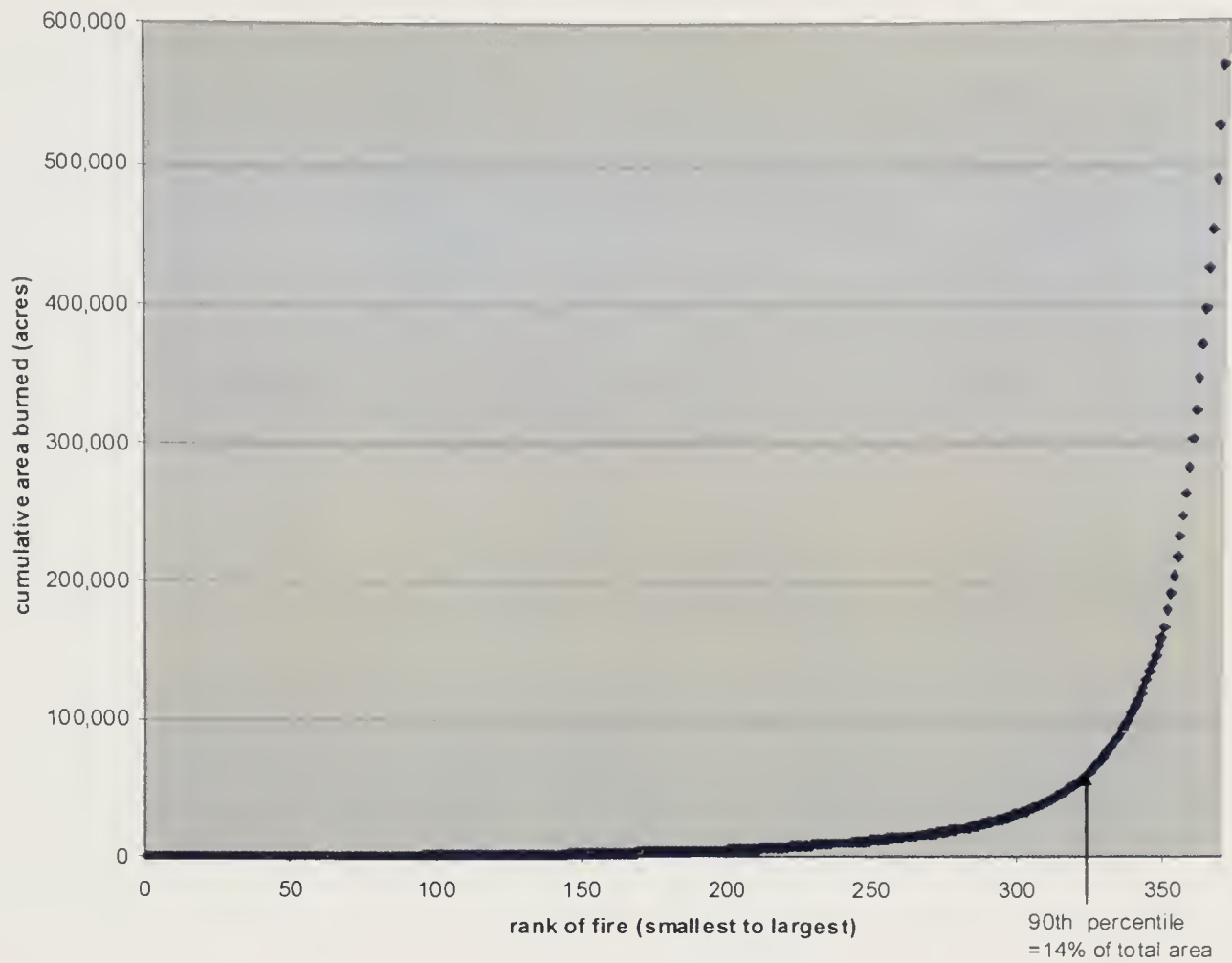
Figure 2. Rank ordered cumulative size distribution
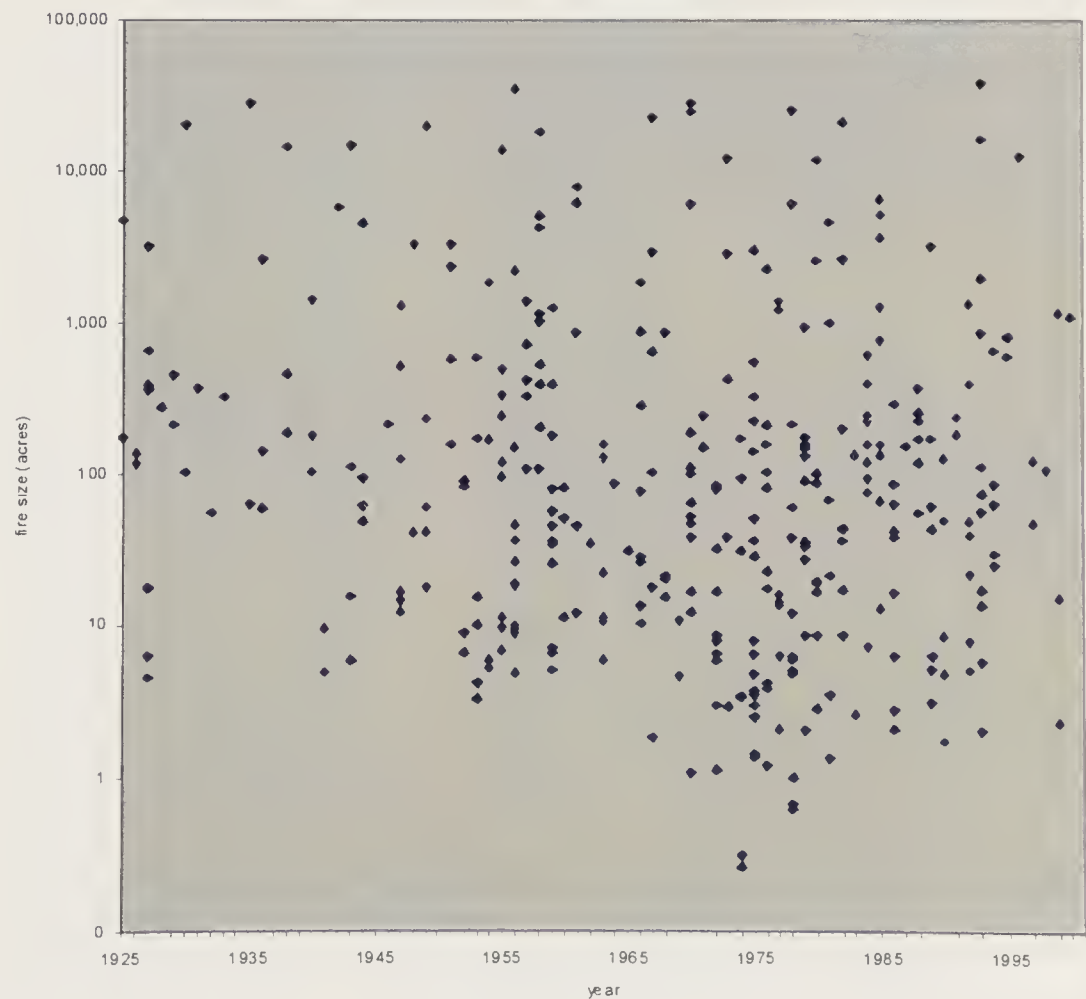1925-2003 (smallest to largest).

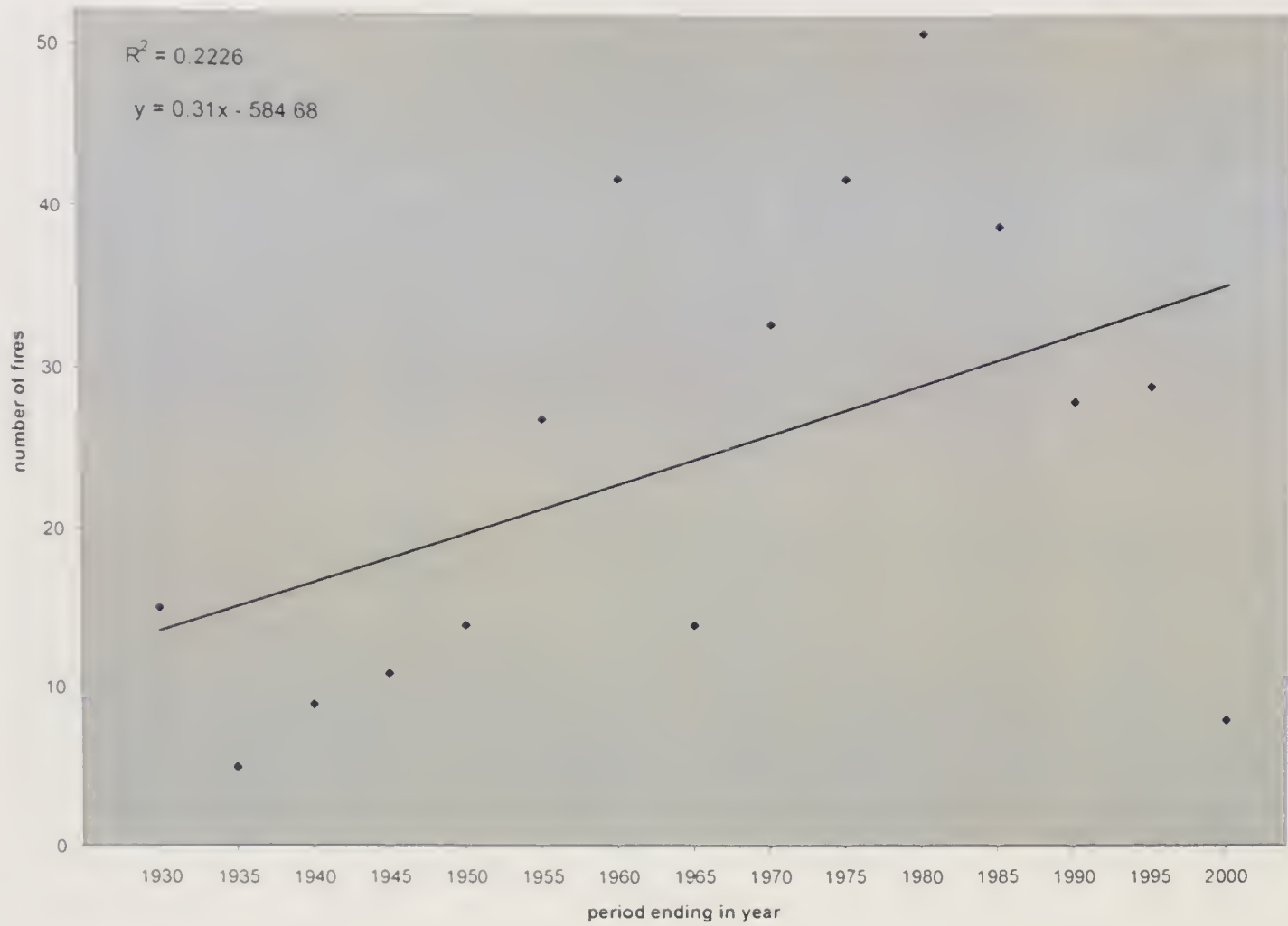
Figure 3. All fires by size and year.
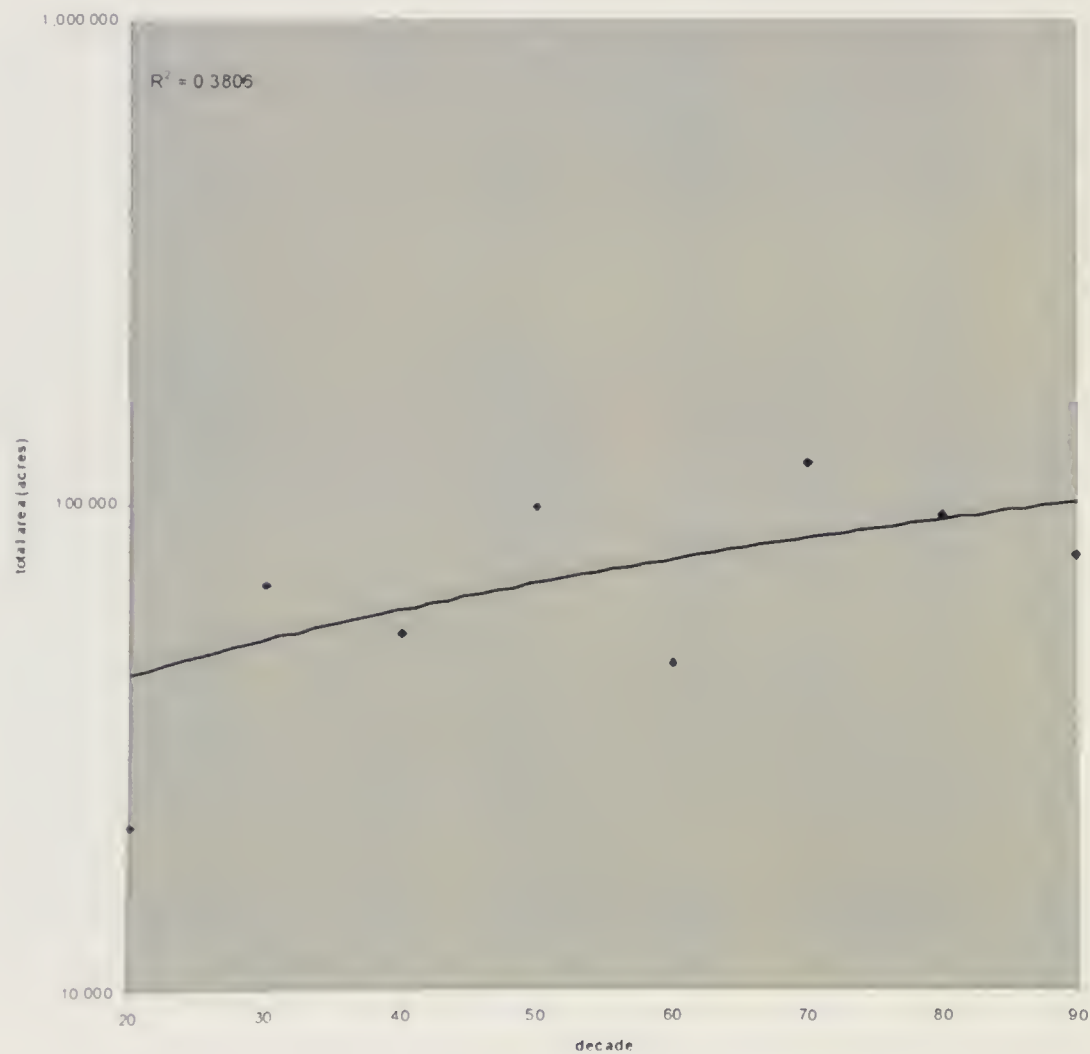
Figure 4. Number of fires 1925-2000.

Figure 5. Total area burned 1925-2000.

FIRE HISTORY 1925 - 2001
Number of Fires Since 1925
Santa Monica Mountains National Recreation Area

CAMARILLO

THOUSAND OAKS

SAN FERNANDO VALLEY

LOS ANGELES

Fire frequency classes in Santa Monica Mountains zone		
# of times burned	area in class (acres)	% of total area
0	40000	2.1%
1	476592	24.9%
2	517183	27.1%
3	473802	25.0%
4	198885	10.4%
5	125460	6.6%
6	39602	2.1%
7	20114	1.1%
8	11989	0.6%
9	1057	0.1%

number of fires since 1925
0   5
1   6
2   7
3   8
4   9, 10

water
developed
undeveloped open space
(no fires recorded)

Santa Monica Mountains NRA boundary
Santa Monica Mountains zone
major roads
County boundary

0 1 2 3 4 5 6 7 8 9 10 Miles

Fire data from County Fire Departments and other sources
Map by Santa Monica Mountains National Recreation Area GIS
Map projection UTM zone 11, datum NAD27

N

Figure 6. The complex mosaic of fire history in the Santa Monica Mountains.

canyons and unidirectional winds (Radtke et al.1982; Figure 7) The east-west spread of fires on the coastal slope may account for the increased fire frequency in this area, as different fires overlap (Figure 6).

Similarly, the high fire frequency corridor through the Malibu Canyon area may be partly a function of the break in the mountain range at Malibu Canyon and the increased wind speeds through this pass, making spread from inland fire starts to the coast more likely at this location.

Vegetation Age Classes

The time since the last fire is a good approximation of the age of the vegetation because many plants and regenerated plant parts will be exactly that old. Figure 8 shows a cumulative area curve for age classes based on time since fire in natural areas of the Santa Monica Mountains. Currently the vegetation is dominated by younger age classes: almost 30% of the vegetation is less than 13 years old, 40% is in the 20-30 year age class, and 25% is in the 30+ age class. Old growth chaparral occurs in only a few pockets that have experienced little or no fire and represents only a tiny fraction (<2%) of the total vegetation.

One consequence of large fires is that very large areas of the landscape are even-aged, creating large homogeneous age classes. Although the fire frequency map shows many overlapping fires in a complex mosaic pattern (Figure 6), the large fires typically overrun smaller fires, obliterating this mosaic and establishing large, even aged tracts (Figure 9).

VEGETATION RESPONSE TO FIRE

The stress of the summer dry period and disturbance by wildfire are two major factors that determine the community structure of chaparral in the Santa Monica Mountains. Postfire regeneration success depends on spring-germinating seedlings and postfire resprouts surviving the summer dry season in the first year after fire, a period of 4-6 months without rain (Davis 1989). The different modes of postfire regeneration are associated with suites of morphological and physiological features related to drought tolerance, because some species must survive the first summer as seedlings while others can draw upon established root systems.

It was recognized early in the study of the California flora that two different modes of reproduction, seeding and sprouting, occur following fire (Jepson 1916). Although terminology varies, the idea has been refined over time to recognize three functional modes of post-fire regeneration: *non-sprouters* (NS), species which are killed and regenerate only from seed, also called obligate seeders; *facultative sprouters*, species which regenerate partly from seed and partly from a percentage of the plant population which resprouts, also called facultative seeders; and *obligate sprouters*, which regenerate only from resprouts with no postfire seedling recruitment, also known as non-seeding sprouters (Wells 1969; Keeley and Zedler, 1978; Keeley et al. 1989; Keeley 1998). The facultative sprouters vary widely in their response and recruitment can occur predominately through seeding or sprouting, depending on species and/or population. A subgroup of the obligate sprouters are *functional sprouters*, species that both resprout and recruit seedlings, but whose seedlings all die in the first year postfire. In the Santa Monica Mountains, representative chaparral species for each functional type are *Ceanothus megacarpus, C. crassifolius, C. cuneatus, C. oliganthus,* and *Arctostaphylos glauca* (non-sprouters); *Ceanothus spinosus, Arctostaphylos glandulosa, Adenostoma fasciculatum, A. sparsifolium,* and *Rhus ovata* (facultative sprouters); *Quercus berberidifolia, Prunus ilicifolia, Heteromeles arbutifolia, Rham-*
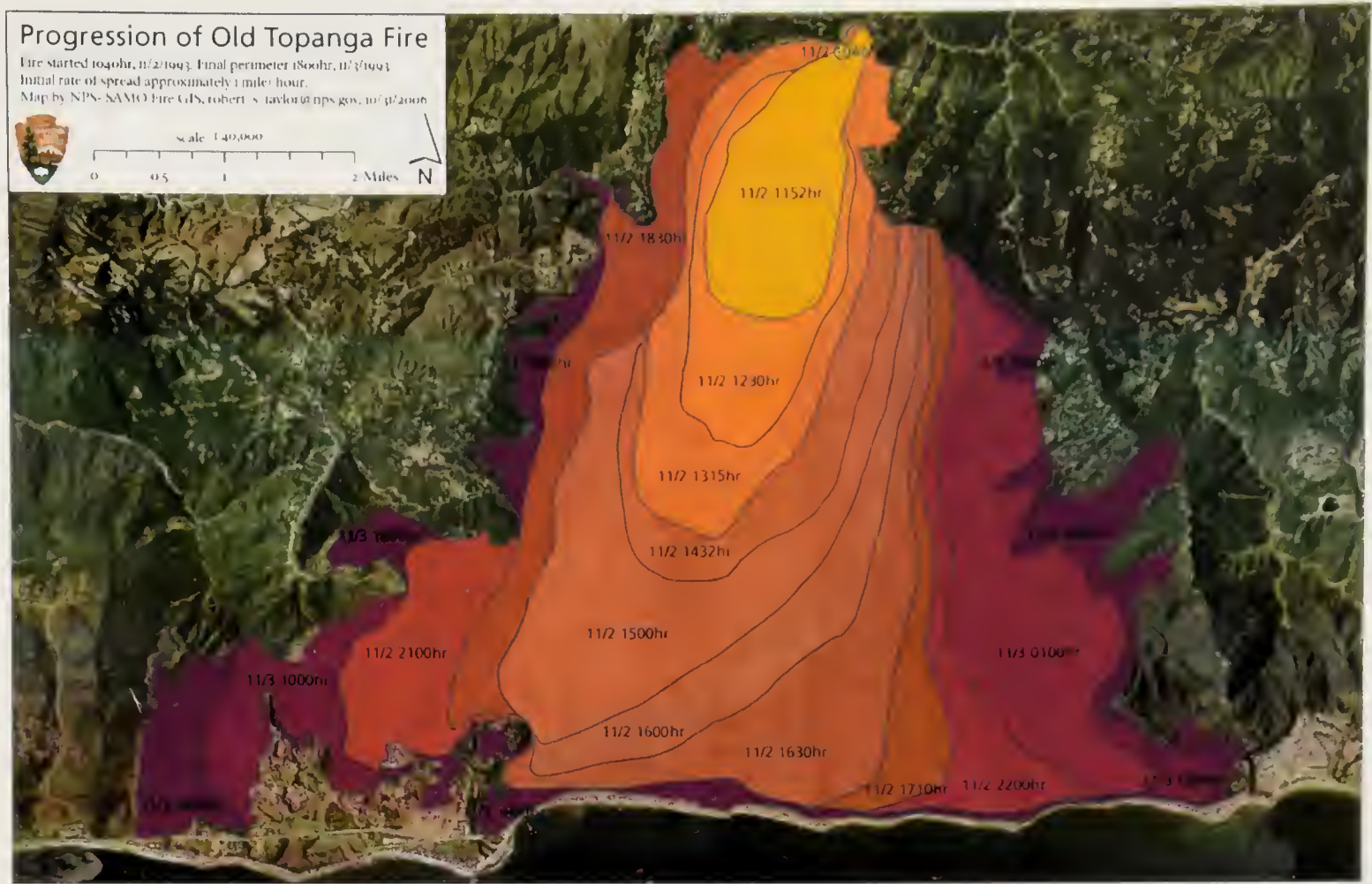
Figure 7. Fire spread patterns are strongly influenced by topography and the direction of the prevailing winds during Santa Ana conditions, as illustrated by the progression of the Old Topanga Fire.
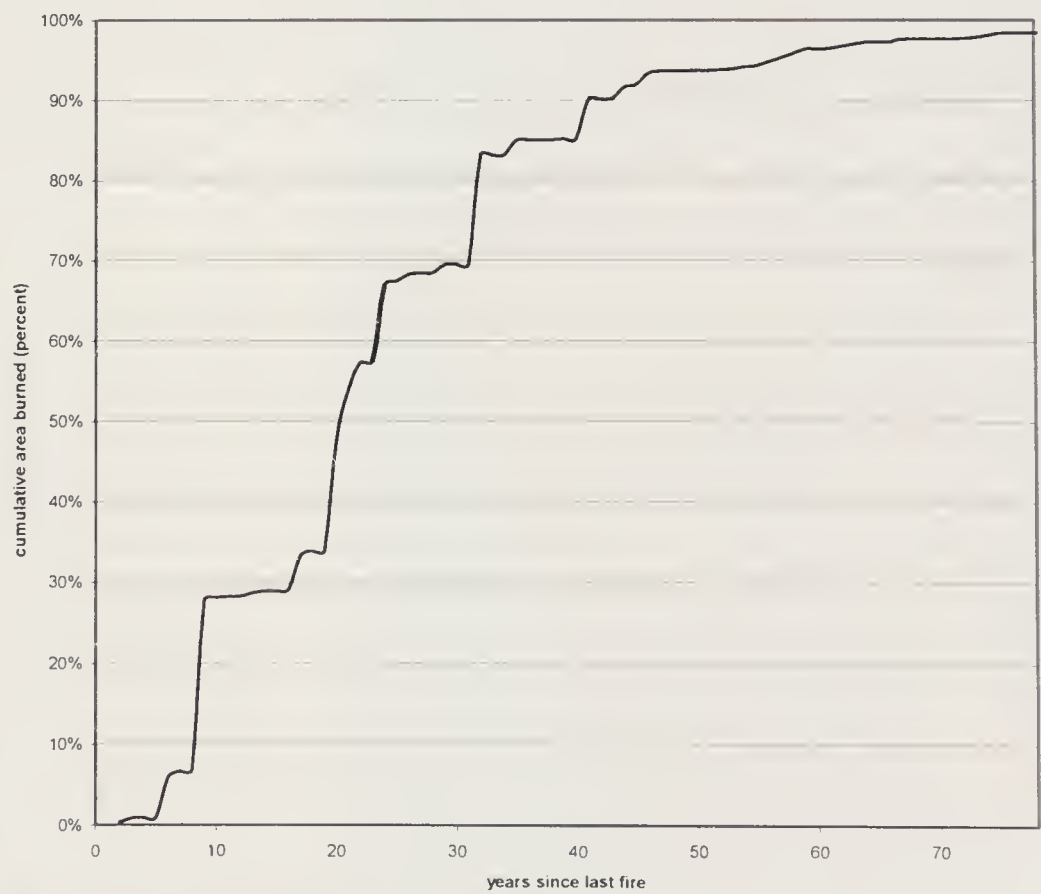

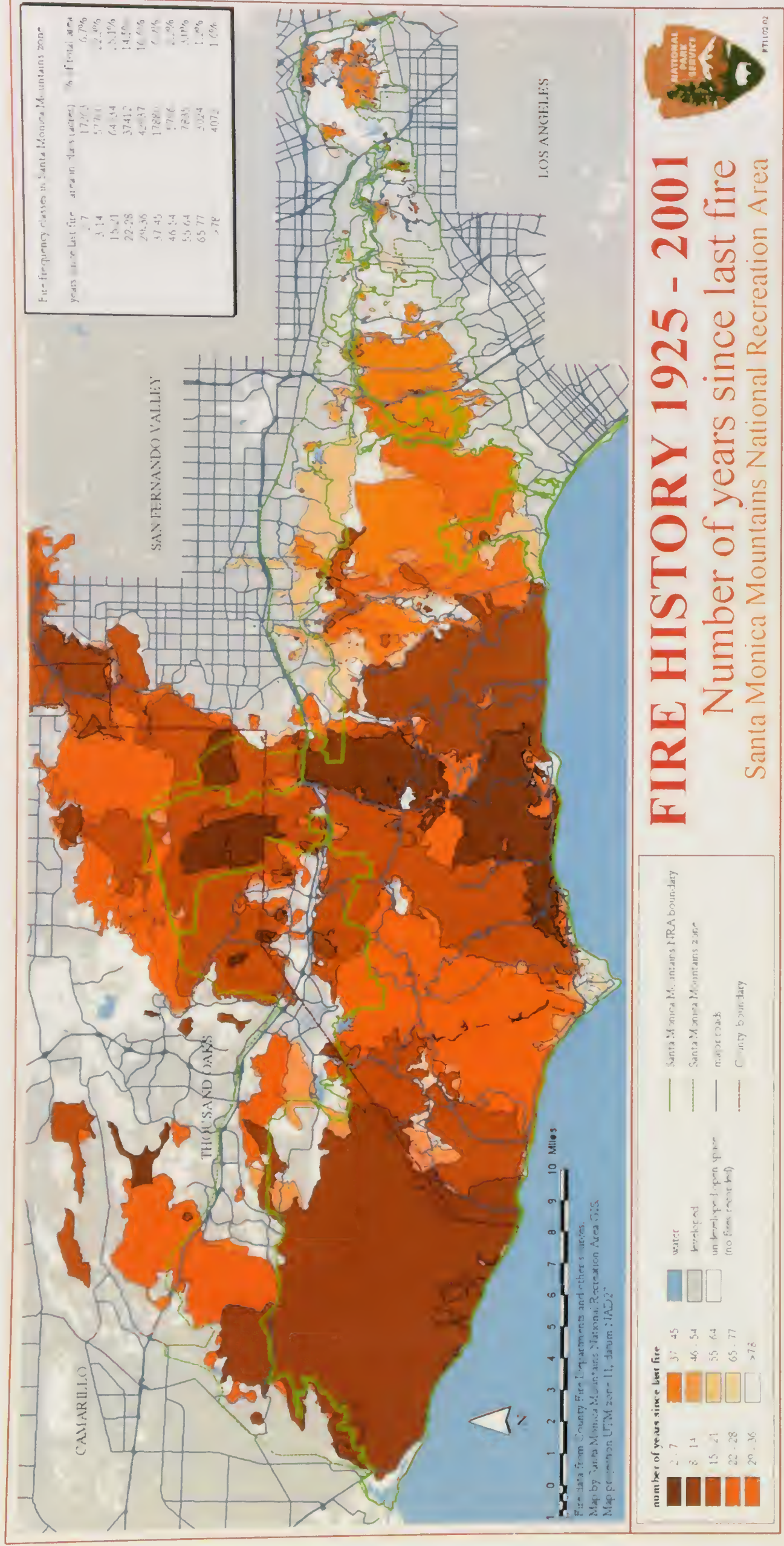**Figure 8.** A cumulative area curve for age classes based on time since fire in natural areas of the Santa Monica Mountains.

Figure 9. Large fires typically overrun smaller fires, obliterating this mosaic and establishing large, even aged tracts.

nus crocea, and *R. ilicifolia* (obligate sprouters); and *R. integrifolia* and *Malosma laurina* (functional sprouters).

Non-sprouting species are shallowly rooted and tolerate high levels of drought stress (Parsons et al 1981; Poole et al 1981; Davis et al. 1998; Jacobsen et al. 2005; Jacobsen et al. *In press*; Pratt et al. *In press*); obligate sprouters are more deeply rooted and reduce drought stress by tapping into deep soil moisture supplies (Poole and Miller 1981; Davis 1989). High seedling mortality occurs in all species in the first summer postfire, but there is a significant difference in survival rates between functional types caused by their differential drought tolerance. Seedlings from non-sprouters have a lower mortality than obligate sprouters and facultative sprouters (Figure 10, from Davis 1989). Seedlings of obligate sprouters die at much lower levels of water stress than non-sprouter seedlings (Oechel 1988; Davis et al. 1998). The profound impact of the physiological attributes of drought tolerance on post-fire population structure is exemplified by *Malosma laurina*. This species vigorously resprouts after fire (99% survival) while also producing an abundant postfire seedling crop (Frazer and Davis 1988, Thomas and Davis 1989). However, this extremely deep-rooted species has a low tolerance of water stress and virtually all seedlings die (99%) in the first summer following a fire (Thomas and Davis 1989; Saruwatari and Davis 1989). Because of its physiology, this species, which is a facultative seeder, behaves as a functional sprouter and is repopulated after fire almost exclusively through vegetative resprouting.

It is clear that an increased capacity to tolerate water stress in terms of resistance to xylem embolism, minimum seasonal water potential, maximum rooting depth, and the hydraulic transport efficiency of stem xylem is correlated to postfire reproductive mode and in part determines postfire resprout success as well as postfire seedling mortality (Figure 10; from Davis et al. 1998). The general geographic distribution of chaparral species is reflected in their relative levels of drought tolerance. The sprouting species of *Ceanothus* and *Arctostaphylos* are more important on mesic slopes and at higher elevations, while non-sprouters reach maximum abundance on south-facing slopes and ridgetops (Schlesinger et al. 1982; Keeley 1986; Nicholson 1993, in Keeley 2000). *Adenostoma, Ceanothus*, and *Arctostaphylos* predominate in the drier areas of the chaparral, but on more mesic sites other broad-leaved, evergreen, resprouting shrubs become dominant (Keeley 2000).

Natural variability in the fire regime interacts with varying regeneration strategies to maintain species diversity. However, if fire frequency exceeds a species' adaptive capabilities, postfire shrub regeneration will be reduced. Sensitivity to fire frequencies varies with regeneration strategies. Non-sprouters show the greatest sensitivity to short fire return intervals and may be eliminated by a single premature burn where insufficient time has passed to build up an adequate seed bank (Biswell 1989; Zedler 1995). Theoretically, non-sprouting species may also be at risk from extinction due to excessively long fire intervals that exceed the life span of both the adults and the seed bank. There is no evidence that long fire intervals are a real problem in California chaparral. One hundred and fifty year old stands of chaparral in the Sierra Nevada recovered as well as younger stands, although populations of the non-sprouter *Ceanothus cuneatus* were reduced (Keeley et al. 2005). In the Santa Monica Mountains, no plant communities are considered to be at risk from an excessively long fire-free period because only 1.6% of the vegetation is more than 77 years old (NPS 2005). Because of the high fire frequency in this region, risk to native plant communities from fire is associated with the potential for repeated fires and short fire return intervals, which exceed the capability of native shrubs to recover after fire (Zedler 1995).

Cm = *Ceanothus megacarpus*
NON-SPROUTER (NS)

Af = *Adenostoma fasciculatum*
As = *Adenostoma sparsifolium*
**FACULTATIVE
SPROUTERS (FS)**

Ml = *Malosma laurina*
OBLIGATE SPROUTER (OS)
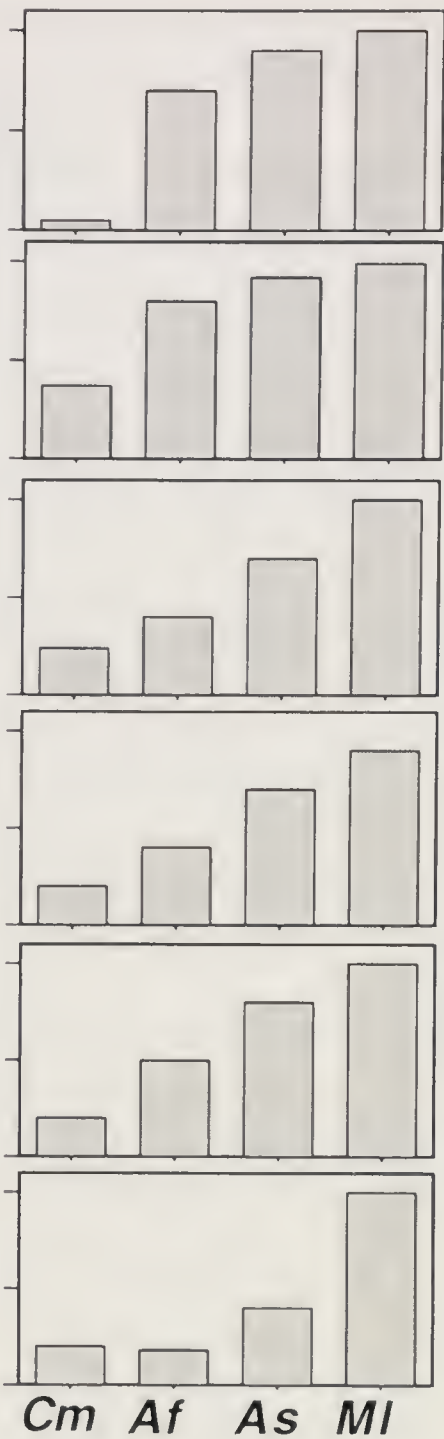
Data from Davis et al., 1998

Figure 10. There is a significant difference in survival rates between functional types caused by their differential drought tolerance.Seedlings from non-sprouters have a lower mortality than obligate sprouters and facultative sprouters.

Vegetation Impacts of High Fire Frequency and Short Fire Return Intervals: The Pepperdine Longitudinal Study

In 1985 the Piuma Fire burned the Pepperdine University Biological Preserve, which had last burned in the 1970 Wright Fire. This fire provided the opportunity to study the interaction of drought tolerance and postfire recruitment demography (Figure 10, from Davis et al. 1998). Initial vegetation recovery followed the classic trajectory expected in chaparral, with abundant postfire native herbs in the first year, widespread resprouting (*Ceanothus spinosus, Malosma laurina*), and seedling recruitment (*Ceanothus megacarpus, C. spinosus, Malosma laurina*). Permanent plots were established to follow the long-term survival of the seedlings and resprouts. After seven years, *Ceanothus megacarpus* (non-sprouter) had 30% survivorship of its seedlings, while *C. spinosus* (facultative sprouter) had 60% survivorship of resprouts, but with a steady decline in seedling survivorship over 5 years to less than 5%. *Malosma laurina* had 98% resprout survivorship, but 99% seedling mortality at the end of the first year and 100% seedling mortality by year two postfire.

In 1993 the Old Topanga Fire burned the site again. With only eight years between fires, the recovery pattern was markedly different. Compared to the 1985 fire, the native herbaceous flora was significantly reduced while the annual non-native grasses increased (Figure 11). This effect on the herbaceous flora has been partly attributed to both higher non-native seed survival under the cooler fire conditions of an early fire and proximity to a non-native seed source such as trails or fuel breaks. *Ceanothus megacarpus* (non-sprouter) was completely eliminated from the site because eight years was insufficient time to reach flowering maturity and to build up a seed bank. *C. spinosus* (facultative sprouter) recruited an extremely reduced number of seedlings because those plants which resprouted after the previous fire were able to grow rapidly and reach reproductive maturity. By year two, all of those seedlings had died. The second fire caused additional mortality in the resprout population of *C. spinosus* and net survivorship declined to 40% three years postfire. *Malosma laurina* (obligate sprouter) resprouts recovered identically to the previous fire with >98% resprout survival. However, similar to *C. megacarpus,* there was no seedling recruitment after the second fire.

Finally, in 1996, the Calabasas Fire burned the site a third time, only three years after the Old Topanga Fire. With this fire the site was irrevocably changed. The native postfire herbs were largely replaced with non-native annual grasses. There were no seedlings of any of the three major shrub species. The *Ceanothus spinosus* resprout population was again reduced, this time to 30%. Based on mortality patterns from the previous two fires, that survivorship would be expected to continue to decline. Only *M. laurina*, with another >98 % resprout survival rate, maintained its pre-1985 population density.

The contrast between a typical stand of closed canopy mixed chaparral (A) and a high fire frequency site that has been type-converted to a non-native grassland dominated by a few resprouting native shrub species (B) is illustrated by the photos in Figure 12.

Impacts of Short Fire Return Intervals: Jacobsen Landscape Study

The Pepperdine longitudinal study demonstrates the impact of repeated short interval fires on plant community structure, especially the potential for extirpation of non-sprouters. An important question is whether the elimination of non-sprouting species has occurred at other sites where there have been short fire return intervals. Jacobsen et al (2004) compared sites throughout the Santa Monica Mountains with short fire return intervals (• six years) to matched control sites where the shortest fire return interval was • 12 years. A point-quarter sampling method was used to measure chaparral shrubs in tandem with a canopy-coverage sampling method for exotic herbs and grasses. Sites that experienced a short fire interval (• six years) contained significantly fewer non-sprouting species and significantly more coastal sage scrub species than adjacent control sites (p = 0.007 for both; Figure 13). The relative densities of facultative or obligate sprouting species and non-native shrub species between short fire interval and control sites were not significantly different (p >0.05; Figure 13). There was a strong correlation between the number of years of the shortest fire return interval and the percent loss in relative density of non-sprouting species relative to the control site (r^2 = 0.94, p = 0.033; Figure 14). A three-year fire interval resulted in complete extirpation, and a six- year interval resulted in an 85% reduction in density. The results were independent of the time since the critical fire interval, which occurred in the 1990's, 1980's, 1970's and 1930's. The failure of the non-sprouters to recolonize is consistent with the observation that non-sprouting shrubs have only limited dispersal ability and, once lost from an area, are extremely slow to recolonize from other established populations (Zedler and Zammit 1989).

Figure 11. Compared to the 1985 fire, the native herbaceous flora was significantly reduced in the 1993 fire, only eight years later, while the annual non-native grasses increased.
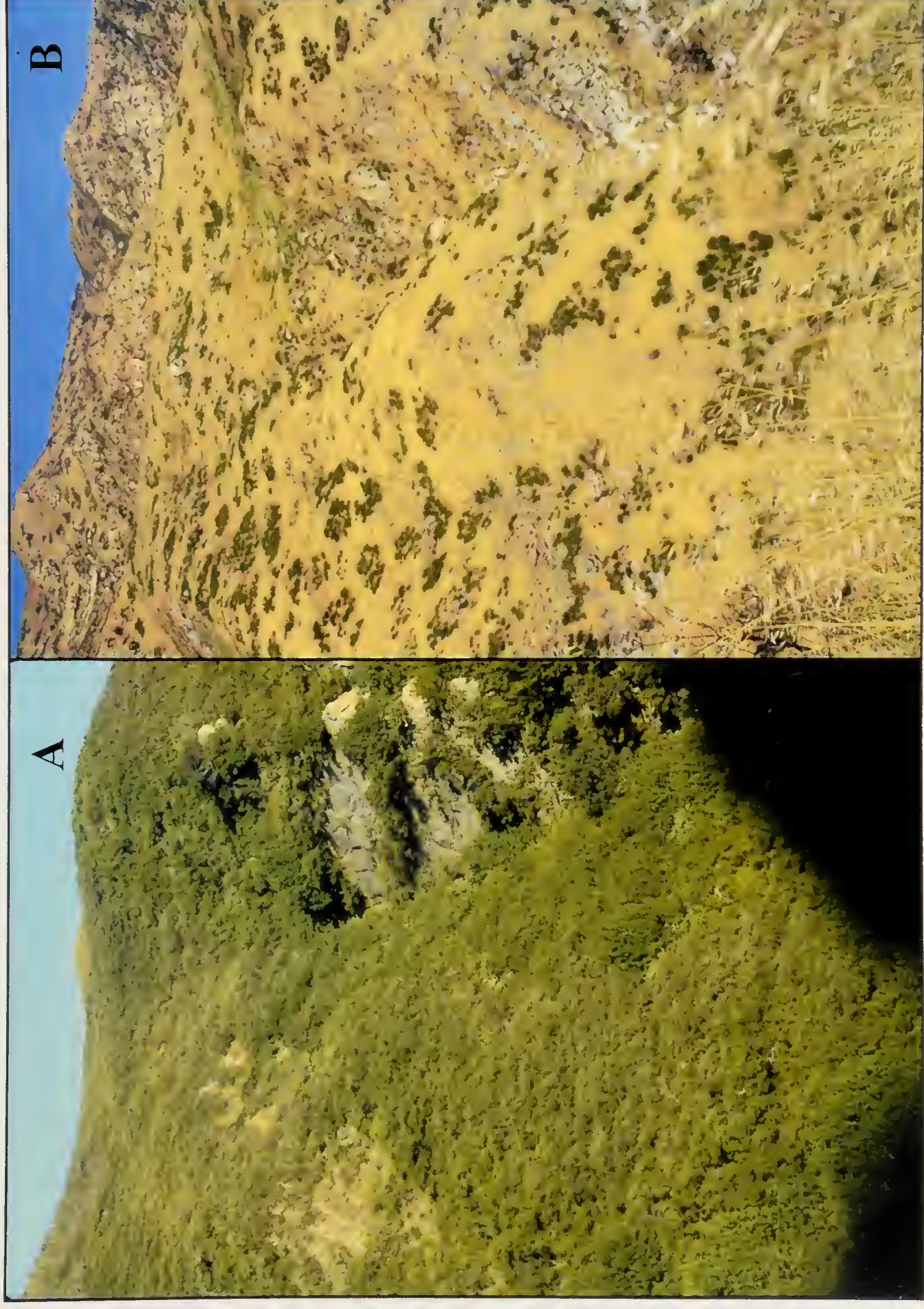
Figure 12. The contrast between a typical stand of closed canopy mixed chaparral (A) and a high firee frequency site that has been type-converted to a non-native grassland dominnated by a few resprouting nativee shrub species (B) (Photos by Steve Davis, Pepperdine University).
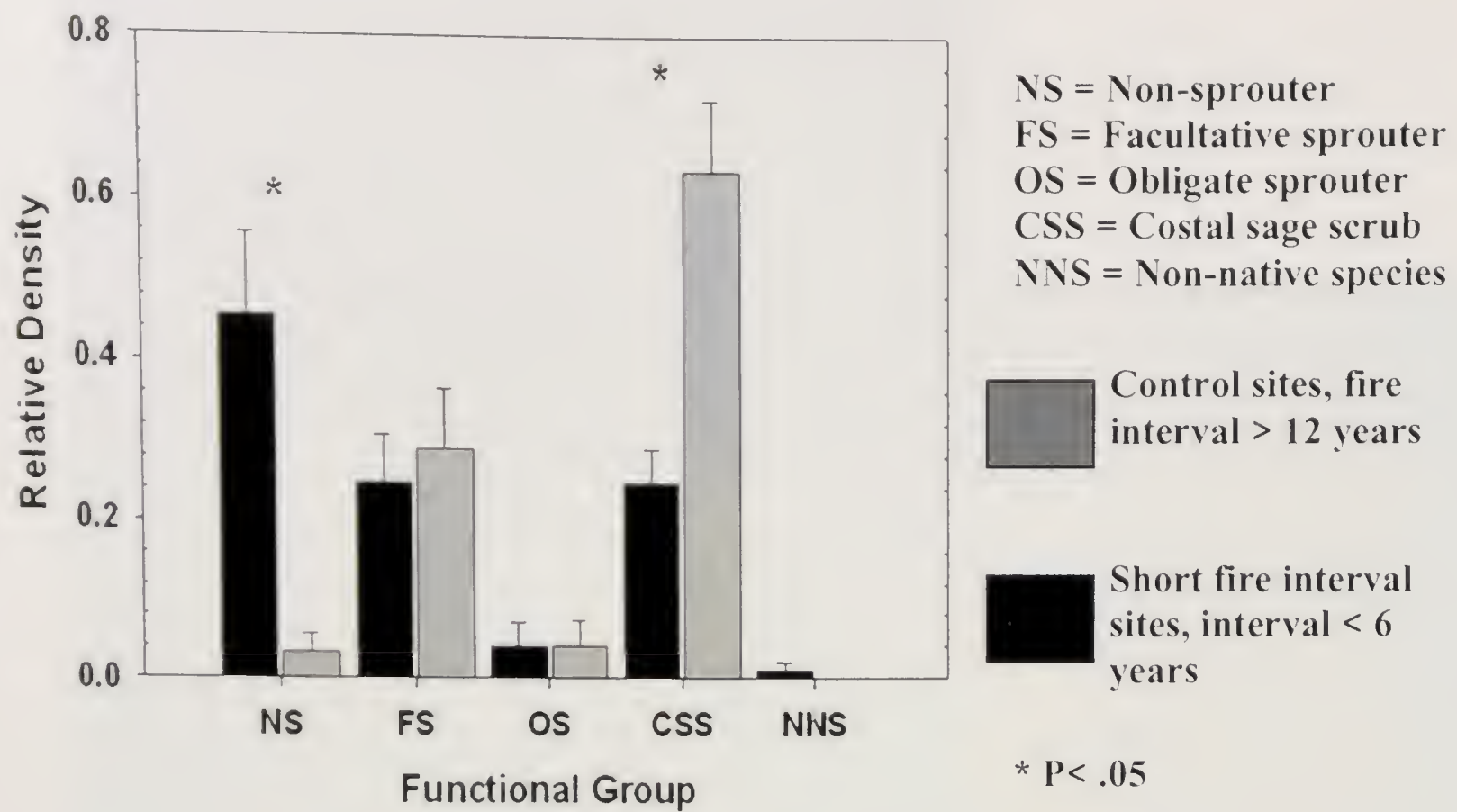
Figure 13. The relative densities of facultative or obligate sprouting species and non-native shrub species between short fire interval and control sites were not significantly different (p >0.05; Figure 10). Data from Jacobsen et al, 2004.
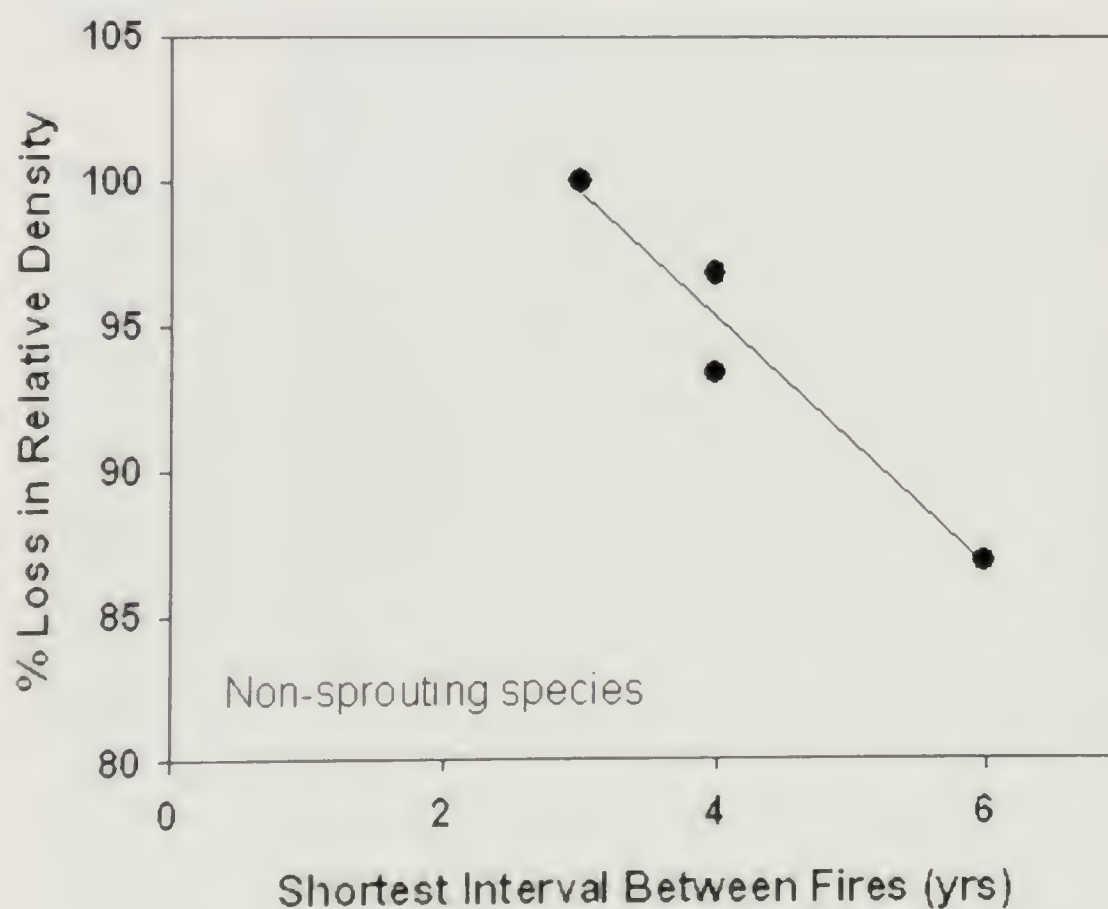

Figure 14. There is a strong correlation between the number of years of the shortest fire return interval and the percent loss in relative density of non-sprouting species relative to the control site ($r^2 = 0.94$, p = 0.033). Data from Jacobsen et al, 2004

While the extirpation of non-sprouting chaparral species is the most obvious effect of high fire frequencies and short fire return intervals, the effects on plant community structure are potentially much more pervasive. Although facultative seeders resprout after fire, mortality of lignotubers can be very high if fire returns prematurely (Zedler et al. 1983; Haidinger and Keeley 1993). Since a premature fire also kills seedlings that germinated in response to the previous fire, facultative seeders show only limited ability to persist under repeated disturbance. Obligate sprouters that show the greatest resilience under short fire return intervals (Zedler et al. 1983; Fabritius and Davis 2000) nevertheless may be severely impacted by sustained high-frequency fire regimes. Successful germination and recruitment of new individuals is correlated with the cooler, moister, low-light conditions and increased litter depth associated with the mature closed-canopy chaparral that develop over fire-free intervals of forty years or more (Lloret and Zedler 1991; Keeley 1992a & b; DeSimone 1995). If a short-interval fire regime is maintained, mature individuals and lignotubers that inevitably perish in fires will not be replaced, resulting in loss of resprouting populations over time (Zedler 1995). Finally, native annuals of the post fire herbaceous flora compete poorly and are eliminated where non-natives become dominant (Keeley 1981).

Type Conversion

The introduction of herbaceous exotics, particularly annual grasses, has fundamentally altered the fire ecology of southern California and plays a significant role in the conversion of shrublands to annual grasslands. Where fires are frequent, non-native herbaceous annual vegetation has been observed to increase and replace shrublands (Vogl 1977; Barro and Conard 1987; Haidinger and Keeley 1993; Beyers et al. 1994). This type conversion of shrubland to annual grassland has been widely observed in California (Keeley 1990; Keeler-Wolf 1995; Minnich and Dezzani 1998).

Annual grasses increase the fire frequency by changing the amount, distribution, and seasonal availability of fuels for fire (Giessow 1997). These grasses complete their life cycle early in the summer season, but do not easily decompose (D'Antonio and Vitousek 1992; O'Leary 1995). This results in a large amount of fine standing dead fuel that supports very rapid rates of fire spread under a broader range of weather conditions than chaparral (Barro and Conard 1987). Dry grasses have the lowest heat requirements for ignition and therefore have the longest fire season and highest fire frequency of any southern California vegetation type (Radtke 1983). Most importantly, the capacity of exotic herbaceous fuels to burn is little influenced by previous fire history. Herbaceous fuel build-up is sufficient to support fire return intervals of one or two years, a cycle that will eliminate shrub communities (Zedler et al. 1983; Nadkarni and Odion 1986; Minnich and Dezzani 1998).

Early fire return creates a positive feedback loop that leads to continued increases in fire frequency and dominance by non-native annuals (Figure 15; from Keeley 2006). When closed-canopy chaparral burns in normal 30-100 year intervals, the result is an intense canopy fire with low alien seed survivorship and strong native herb and shrub recovery. This will eventually return to closed canopy chaparral. If fire returns too early, then it will be of lower intensity and alien seed survivorship will be high (Moreno and Oechel 1991). Non-sprouting species would then be lost, resulting in degraded chaparral with more open canopy of native resprouters and a dense understory of native and non-native annuals and grasses. The altered vegetation is more conducive to another fire because of the high herbaceous fuel component. If repeat fires occur, they will lead to chaparral type conversion to non-native grassland with remnant resprouting shrubs and non-native annual grasses (Keeley 2006). In areas near fuel breaks, the amount of non-native cover in areas with three or more fires increased 25% over areas with one or no fires (Merriam et al 2006).
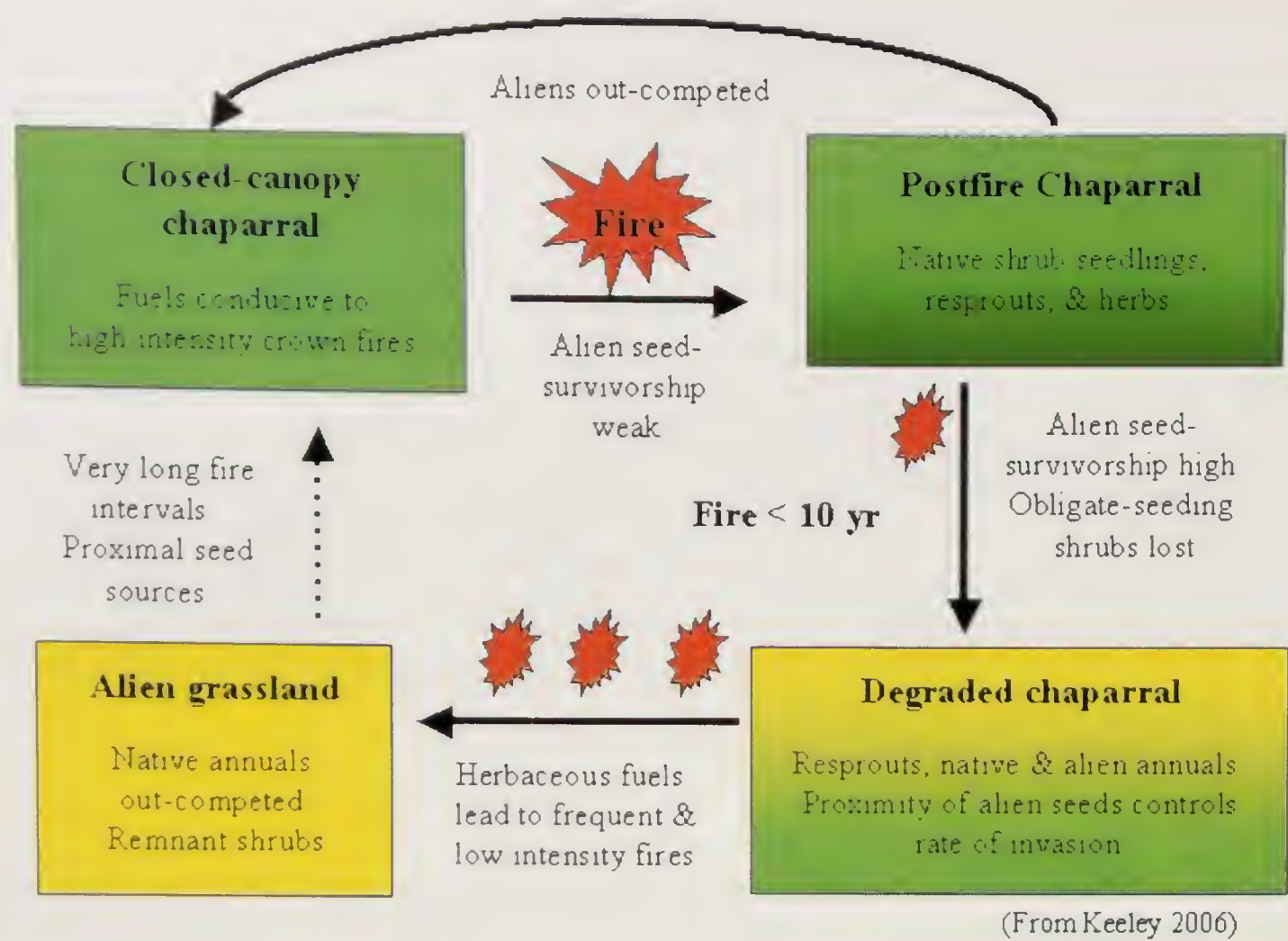
Figure 15. Natural fire cycle, 30-100 years.

Future Threats to Native Plant Communities

Many areas of the Santa Monica Mountains appear to have experienced some degree of fire-driven type conversion (Figure 16). NPS has calculated that 19% of the National Recreation Area has experienced a minimum fire return interval of less than six years, 25% has had minimum fire return intervals between 7-12 years, and the remainder has had a minimum fire interval of greater than 12 years. As population growth continues in the Santa Monica Mountains, urban development will increase the fire frequency and decrease the average fire return interval. Syphard et al. (2007) have modeled urban growth and fire disturbance to compare the relative impacts of altered fire regime and direct habitat loss to different functional plant groups: Coastal Sage Scrub (CSS), Non-Sprouting Chaparral Species (NS), and Obligate Sprouting Chaparral Species (OS). CSS and OS are most vulnerable to direct habitat loss, while NS are susceptible to both altered fire regimes and direct habitat loss. The cumulative effects of repeated fires may occur gradually as urban development expands across the landscape. With development there is likely to be a shift in the location of ignitions and fires, creating a lag time before the cumulative ecological effects of increased frequencies and shorter fire return intervals are observed.

CONCLUSIONS

The impacts of fire in chaparral have been misunderstood because of the habitat's apparent high resilience to fire and the inappropriate transfer of the forest model of the Ponderosa pine fire regime to chaparral fire management. The Santa Monica Mountains provide a model for how changes in the fire regime driven by urbanization and habitat fragmentation can alter native plant communities. The relationship of plant physiological traits to functional modes of post-fire regeneration provides a means to understand the future trajectory of our native plant communities in response to altered fire regimes.

Figure 16. An example of fire type conversion in the Santa Monica Mountains.

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